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THE FOOD, FEEDING, AND DEVELOPMENT OF YOUNG TUFTED AND HORNED PUFFINS IN ALASKA

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ABSTRACT.—Aspects of nestling Tufted Puffin (*Fratercula cirrhata*) and Horned Puffin (*F. corniculata*) feeding ecology, growth rate, and fledging success were studied on Buldir Island, Alaska, in 1975 and on Ugaiushak Island, Alaska, in 1976 and 1977. Growth rates were measured for single wild chicks given supplemental food, single chicks raised in captivity and fed ad libitum, and for artifically twinned chicks with and without supplemental food and for twinned chicks raised in captivity. Data from these colonies and years (colony years) were compared with those from other colony years for these species and for Atlantic Puffins (*F. arctica*). For most aspects of nestling feeding ecology that have been measured, available data are too variable (seasonally, annually, or geographically) to give a reliable correlation with feeding conditions. Growth rates equal to 1.5% of adult body weight/day or less were associated with poor feeding conditions while growth rates of 2.5% or more represented optimum feeding conditions. Nestling growth rates currently provide the best means of assessing feeding conditions. The implications of puffins' ability to raise two chicks, rather than their normal clutch of one, are also discussed.

Local seabird populations in Alaska may well be affected by the development of offshore oil and gas resources. Recognizing this, the U.S. Bureau of Land Management, through interagency agreement with the National Oceanic and Atmospheric Administration (NOAA), sponsored the Outer Continental Shelf Environmental Assessment Program (OCSEAP) to obtain baseline data on the distribution and abundance, breeding biology, and feeding ecology of certain Alaskan seabird species. These data were to be used in making management decisions and as a standard against which post-development data could be compared. If the consequences of petrochemical exploitation are to be predicted and safeguards established against potential problems, the ecology of the species most likely to be affected must be known (McKnight and Knoder 1979).

Between 40 and 50 million seabirds of at least 35 species breed in Alaska (Sowls et al. 1978). Alcids (Family Alcidae) comprise at least 65% of these, of which approximately 20% are puffins (Sowls et al. 1978): Tufted Puffins (*Fratercula cirrhata*), Horned Puffins (*F. corniculata*), and Rhinoceros Auklets (*Cerorhinca monocerata*)—actually misnamed puffins (Storer 1945). Of the 176 species of birds using marine habitats in Alaska, British Columbia, and Washington, Tufted and Horned puffins rank among those most vulnerable to oil pollution (King and Sanger 1979). In addition, they may be affected by changes in the distribution and abundance of their prey caused by offshore oil and gas development.

Tufted and Horned puffins are diurnal, pelagic seabirds that measure about 390 and 350 mm in length, respectively. They nest in underground burrows or rock crevices on steep sea slopes, along cliff-edges, or in talus slopes. Both sexes have two brood patches, but females typically lay only one egg, which is incubated for six to seven weeks. Puffins capture prey (primarily small fish and invertebrates) by pursuit diving, and feed whole prey to their semi-precocial young for six to seven weeks. Information on their habits is given by Dawson (1913), Willett (1915), Bent (1919), Dement'ev and Gladkov (1951), Kozlova (1957), Gabrielson and Lincoln (1959), Swartz (1966), and Sealy (1973a).

My purposes here are: (1) to present the results of studies I conducted for OCSEAP on the feeding ecology (food, feeding, and development) of nestling Tufted and Horned puffins on Ugaiushak Island, Alaska, in 1976 and 1977 and from a study I conducted on Buldir Island, Alaska, in 1975; (2) to compare my results with those for these species in other colonies and years (colony years) and with those for Atlantic Puffins (*F. arctica*); (3) to describe and summarize the current data for the major components of nestling Tufted and Horned puffin feeding ecology in Alaska; and (4) to identify those components of nestling feeding ecology that might best be used in future studies to detect possible effects of offshore oil and gas development on puffin feeding conditions (e.g., availability and abundance of suitable prey).

Fledging success provides the best measure of the reproductive health of a population but it is sometimes influenced by factors unrelated

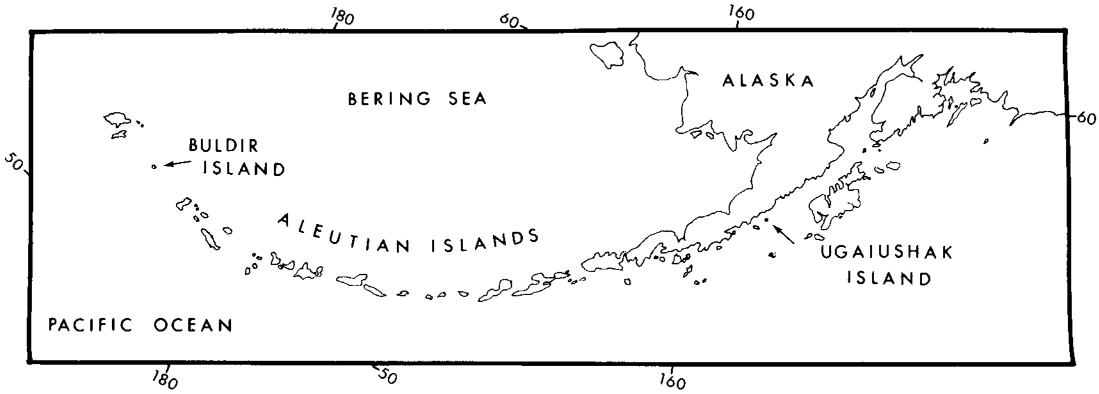

FIGURE 1. Location of Ugaiushak Island and Buldir Island, Alaska.

to feeding conditions. Because young birds appear to be sensitive to regional and annual variations in feeding conditions (Ricklefs and White 1975), their growth rates provide a better criterion by which feeding ecology data from pre- and post-offshore development studies can be compared. Since puffin growth rates varied among colony years, I had to develop a standard for making comparisons. I attempted to provide such a standard by correlating observed growth rate with apparent feeding conditions and by determining the maximum growth rate chicks could obtain. Feeding conditions were assessed and maximum growth rates were estimated by measuring the growth of single chicks and artificially twinned chicks raised in situ and given supplemental food, and of chicks raised in captivity and fed ad libitum. The twinning experiments also provided information on the birds' ability to raise a second young.

STUDY AREAS

Ugaiushak Island (56°47′N, 156°41′W), in the western Gulf of Alaska, is one of many small islands harboring seabird colonies along the Alaska peninsula (Fig. 1). It was chosen as an OCSEAP study site because of its proximity to areas being considered for offshore oil and gas development and because of its rich diversity and abundance of breeding seabirds. Fifteen species of seabirds, totaling over 56,000 birds, breed on Ugaiushak, including approximately 14,000 Tufted Puffins and 18,000 Horned Puffins (Sowls et al. 1978). Ugaiushak (ca. 175 ha) consists of two land masses—hereafter called East Island and West Island—connected by a narrow isthmus. East Island is relatively flat with a maximum elevation of 30 m; West Island has three peaks located on the southwestern end of the island (the tallest being 170 m), a central ridge, and a gently sloping plain across its northwestern end. East Island supports lush *Calamagrostis* grassland and mixed-meadow communities; these also occur on West Island with an extensive heath community. Sea cliffs rising to 100 m comprise most of Ugaiushak's western and southern coastlines. Tufted Puffins nest almost exclusively in earthen burrows along the tops of these cliffs where the island's soil is deepest. Gradually sloping ledges, beach boulders, and talus slopes make up the eastern and northern coasts; here, Horned Puffins principally use rock crevices for nest sites.

Buldir Island (52°21′N, 175°56′E), the westernmost member of the Rat Island group of the Aleutian Islands, is the most isolated of the Aleutians, being 113 km west of the nearest island (Fig. 1). Over 1.8 million seabirds of 20 species breed on Buldir, including approximately 20,000 each of Tufted and Horned puffins (Sowls et al. 1978). My study of puffins on the island was ancillary to an ongoing U.S. Fish and Wildlife Service research project on the endangered Aleutian Canada Goose (*Branta canadensis leucopareia*).

With an area of about 2,000 ha, Buldir's topography is dominated by three volcanic peaks, which range in elevation from 539 to 655 m; the remainder of the island being lesser peaks and rolling hills. Buldir is heavily vegetated, except at the highest elevations, with moss-willow tundra and *Elymus*-umbel communities whose plants reach over 2 m in height by late summer. The 20-km coastline consists chiefly of large boulder or gravel beaches or talus slopes, backed by steep sea slopes or cliffs. Most Tufted Puffins nest in earthen burrows on sea slopes, but some nest in the rock crevices of talus slopes. Most Horned Puffins nest in rock crevices of talus slopes and among beach boulders, with some nesting in earthen burrows on sea slopes or on the banks of inland creeks. My study plots for Tufted Puffins were primarily on the sea slopes at the northwest end of the island and for Horned Puffins on the Main Talus, located on the north-central side of Buldir. Observations of daily feeding activity were made on the Main Talus where several thousand pairs of both puffin species and tens of thousands of pairs of *Aethia* auklets nest.

METHODS

Investigations were conducted on both species at Buldir from 17 May to 5 September 1975, and at Ugaiushak from 24 May to 2 September 1976 and from 23 April to 29 August 1977. In 1976, investigations of Horned Puffins were secondary to those of Tufted Puffins.

Eight components of nestling feeding ecology were studied for both species but not in each colony year: food delivery, feeding frequency, prey species composition of food loads in the bill, prey size, food load size and weight, growth rates, and fledging success. I selected these components because, with the possible exception of food delivery, they seemed to have the potential to vary in response to feeding conditions.

FOOD DELIVERY

Canvas blinds erected within the breeding colonies of both species before egg-laying began allowed me to view, at close range (1 — 10 m), nest site entrances and to monitor the coming and going of adults. Tufted Puffin burrows, which measured from 0.5 to >3.0 m long, were marked with numbered tongue depressors and colored flags; at each, I made a small access hole (ca. 10 cm diameter) into the enlarged nest chamber, usually located at the rear of the burrow. Each hole was kept plugged by a wedge-shaped piece of sod that could readily be removed. Horned Puffin nest sites were similarly marked; access to nests was provided by natural openings among the rocks. When a food-carrying adult entered a marked nest site, I immediately left the blind and looked into the nest.

FEEDING FREQUENCY

Estimates of feeding frequency for individual Tufted Puffin chicks on Ugaiushak were based on observations of birds delivering food to marked burrows and on the results of monitoring burrows using toothpick "gates" (see Boersma and Wheelwright 1979). I watched from a blind during sessions of 2–8 h conducted at least three days per week throughout the nestling period in both years. Toothpick gates were placed at the entrances to 10 burrows containing chicks, once in early and again in late August each year. Toothpicks were left in place until displaced.

Daily feeding activity of Tufted and Horned puffins on Buldir was studied during all-day watches from a blind on Main Talus on 12 and 22 August. On these dates, the average chick age was approximately 2.5 weeks for Tufted Puffins and approximately 4 weeks for Horned Puffins (Wehle 1976), roughly corresponding with the ages of Atlantic Puffin chicks during their period of peak growth (Harris 1978). Thus, I expected that feeding frequency would probably increase between these two dates to meet the increasing nutritional requirements of the chicks. Watches were made at 15-min intervals from approximately 0.5 h before sunrise to 1 h after sunset. (Preliminary observations indicated that puffins did not feed their young at night.) Each watch consisted of counting for 1 min the numbers of puffins of each species with and without food in the bill that flew past a given point on a colony. In the analysis, data from two consecutive watches, beginning at sunrise, were pooled into 0.5-h intervals and the few birds observed before sunrise and after sunset were included in the first 0.5-h interval after sunrise and before sunset, respectively.

PREY SPECIES COMPOSITION OF BILL LOADS, PREY SIZE, AND BILL LOAD SIZE AND WEIGHT

Adult puffins carry their prey crosswise in their bills back to their nests. These loads of food can be collected and their contents weighed, measured, and identified.

On Ugaiushak, I collected Tufted Puffin bill loads from burrows provided with access holes and monitored from a blind. When a food-carrying adult entered one of these burrows, I immediately left my blind, opened the access hole, and retrieved the food sample. To determine if prey species composition of loads, prey size, or load size and weight varied during the nestling period, I collected 41 samples from 10 monitored burrows from 3–14 and from 19–30 August in 1976 and 31 samples from 44 monitored burrows from 10–15 and 21–27 August in 1977. Collections were made during all hours of the day and sometimes from the same burrow in the same day. In 1977, I also determined, using 10 × 50 binoculars, the prey species and number of prey for 33 bill loads carried by Tufted Puffins.

On Buldir, I collected 15 loads each from Tufted and Horned puffins between 14 and 21 August. Loads were obtained primarily by catching food-carrying adults in mist-nets placed over nest entrances; a few food-carrying adults were also shot and their bill loads collected.

General information on the nestling food of

Horned Puffins on Ugaiushak came from observations of dropped fish found within their colonies and from observations of bill loads being carried by adults. Accessible Horned Puffin nest sites on Ugaiushak were usually far apart, thereby allowing only a few nest sites to be monitored simultaneously from a blind; I therefore decided not to collect Horned Puffin food loads.

All loads collected were weighed to the nearest 0.5 g; individual prey were counted and measured to the nearest 1 mm (fish from the tip of the snout to the tip of the caudal fin, and squid from the anterior end of the mantle to the tip of the longest tentacle). Most of the fish were identified by me; other prey were preserved in 5% formalin and later identified by the staff of the Aquatic Collections, University of Alaska Museum, Fairbanks.

GROWTH RATES

During the three colony years on Ugaiushak and Buldir combined, I measured the growth rates of 67 Tufted Puffin and 26 Horned Puffin chicks reared under natural and experimental conditions. Chicks raised under natural conditions hereafter are called "unfed singles." Experimental chicks included single chicks given supplemental food ("fed singles"), artificially twinned chicks with and without food ("fed" and "unfed" twins, respectively), and single and twinned chicks raised in captivity and fed ad libitum ("captive singles" and "captive twins," respectively). Growth rates of chicks raised under the various conditions were intended to provide information on feeding conditions, the maximum rate that chicks could attain, and the ability of adults to feed more than one young. Interpretation of these data was based on assumptions that: (1) the amount of supplemental food given to chicks alone was insufficient to enable chicks to reach maximum growth rates; (2) the amount of supplemental food plus the amount of food delivered by adults would be equal to or greater than that needed for chicks to attain maximum growth rates; and (3) captive chicks fed ad libitum would grow at maximum rates. For chicks receiving supplemental food, I also considered whether or not a feedback mechanism existed between chicks and adults such that certain chick behavior stimulated adults to deliver food.

Fed singles would presumably grow faster than unfed singles if feeding conditions were suboptimal (i.e., if adults were unable to provide chicks with sufficient food for maximum growth) and at the same rate as unfed chicks if feeding conditions were optimal. With a feedback mechanism, any supplemental food I provided would moderate the chick's behavior so that adults would deliver food only if the chick indicated that it was still hungry. In this situation, the chick would receive as much food as it could use and grow at a nearly maximum rate. Without a feedback mechanism, the amounts of food delivered by adults would be inherent to their feeding behavior as influenced by feeding conditions. A chick reared under these circumstances would grow at nearly the maximum rate if feeding conditions were optimal, but more slowly if feeding conditions were less favorable. For fed twins, I expected the results to be similar to those for fed singles, except that the growth rates of twins would be even more sensitive to food shortages.

For unfed twins, if a feedback mechanism was operative, then the adults would have twice the normal pressure to supply food; these chicks would grow more slowly than unfed singles unless feeding conditions were excellent. In the absence of a feedback mechanism, adults would deliver only the amount of food normal for a single chick and the twinned chicks would grow more slowly than unfed singles, regardless of feeding conditions.

I measured growth rates by weighing chicks to 0.5 g (under 100 g) or to 1 g (100+ g) every second or third day on Ugaiushak and daily on Buldir from hatching until either fledging or my departure from the island.

Food supplements consisted of fresh fillets of black rockfish (*Seabastes melanops*) and small whole fish, primarily Pacific sand lance (*Ammodytes hexapterus*) and capelin (*Mallotus villosus*). Fed singles received 50 g of food supplement once daily beginning at three days of age; fed twins together received 50 g of food supplement once daily when three to seven days old and 100 g daily thereafter. Supplemental food was placed at the entrance to the nest chamber for Tufted Puffins and near the nest for Horned Puffins.

Twins were artificially created by adding a chick from one nest to another containing a single chick; chicks were twinned when less than two days old. Captive chicks were removed from their nests when two to five days old and raised outside in wood and burlap simulated burrows. All captives were fed ad libitum the same prey used for food supplements plus a commercial brand multi-vitamin and multi-mineral supplement.

FLEDGING SUCCESS

Due to ship scheduling, I left each island each year before all puffins had fledged. Therefore, I estimated fledging success from (1) the proportion of nestlings initially monitored that had fledged or were of fledging weight at the time of my departure, and (2) a subjective evaluation of the growth rates of chicks not of fledging weight at the time of my departure. I considered fledging weight of Tufted Puffins to be 496 g, the minimum weight of any chick known to have fledged on Ugaiushak in 1976 or 1977, and of Horned Puffins to be 400 g, the lowest fledging weight reported by Amaral (1977).

STATISTICAL ANALYSIS

A chi-square test was used to test for homogeneity in the relative numbers of (1) birds observed carrying food during all-day watches on 12 and 22 August 1975, and (2) individual sand lance, capelin, and gadids in bill loads between early and late August and between years.

Prey size and bill load size and weight were compared by the Mann-Whitney test (W) for samples within the same colony year and by the Kruskal-Wallis (*H*) and a posteriori Dunn tests (Dunn 1964) for samples among colony years.

Growth rates for chicks in my studies were analyzed by the Mann-Whitney test and Kruskal-Wallis test on the median weight-gain/day (g), during the interval from 5 to 30 days of age, for chicks raised under each of the various conditions. For the analysis of twins, I averaged the weight gains of the two chicks in each set, so that the appropriate error was the nest-to-nest variability. Growth rates of unfed single chicks were also analyzed by Ricklefs's (1967) graphical method so that they could be compared more easily with previously published growth rates of Tufted and Horned puffins and other alcids analyzed by this technique (Sealy 1973b, Manuwal and Boersma 1977, Vermeer and Cullen 1979).

I computed growth rates presented in Table 8 from data provided by other investigators (cited in other tables), except for those on the Barren Islands, which were calculated by Manuwal and Boersma (1977).

By Ricklefs's (1967) method, growth data for all colony years best fit the logistic equation. However, as pointed out by Sealy (1973b), the actual growth curves of alcids in the later stages of development do not conform well to the logistic equation and therefore, the goodness of fit depends to some extent on subjective consideration of which data to include. In Ricklefs's terminology, the equation for the logistic curve is: $dW/dt = KW(1 - W/a)$, where W is the weight of the growing bird, a is the final weight (asymptote), t is time, and K is the growth constant (representing overall growth rate) derived by the fitted logistic equation. In

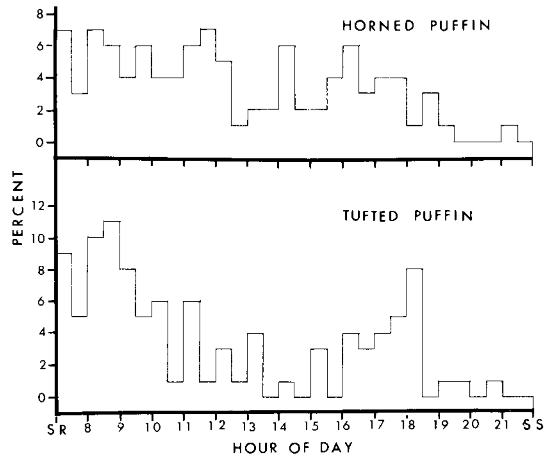

FIGURE 2. Percent of total numbers of food-carrying Tufted Puffins (n = 80) and Horned Puffins (n = 307) observed during half-hour intervals from sunrise (SR) to sunset (SS).

addition to the K value, I also expressed growth rates in terms of Hussell's (1972) instantaneous growth rate, $KR/4 \times 100$ (percent of adult body weight/day), which occurs at the inflection point of the fitted logistic curve.

RESULTS AND DISCUSSION

FOOD DELIVERY

I was often able to remove the sod plugs of Tufted Puffin burrows or to position myself within rock crevices beside Horned Puffin nests so as to observe puffin activity within the nests while remaining undetected. Tufted and Horned puffin chicks received their first loads of food when less than one day old. In each of two Horned Puffin first-food deliveries that I observed, the load consisted of two sand lance, each approximately 60 mm long. Adults dropped food on the nest floor near the chick for the first week and usually near the nest site entrance thereafter. The amount of time adults spent underground when delivering food decreased from several minutes during the brooding period (0–3 days for Tufted Puffins and 5–7 days for Horned Puffins [Wehle 1980]) to less than 10 s in later weeks. Occasionally, I saw adult Tufted and Horned puffins accompany their food delivery by specific behavior, particularly when chicks were less than one week old. For both species, this behavior included the bird lowering its head and moving it slowly from side to side while uttering a faint, low-pitched "errr" sound. Whenever an adult entered the nest, chicks (both species) called loudly and frequently and assumed a food-begging posture, crouching low to the ground and sometimes partially spreading their wings. Once a chick had eaten, it usually ceased calling.

TABLE 1. Number and percent occurrence of prey in bill loads delivered by Tufted Puffins during various Alaskan colony years.

Prey species	Buldir Island 1975		Ugaiushak Island 1976		Barren Islands 1976		Ugaiushak Island 1977		Barren Islands 1977		Cathedral Island 1977		Middleton Island 1978	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Pacific sand lance (*Ammodytes hexapterus*)	23	36.5	370	88.8			287	82.0	46	30.3	86	25.8	39	60.0
Capelin (*Mallotus villosus*)			11	2.6	104	94.5	42	13.0	86	57.0	215	64.9		
Walleye pollack (*Theragra chalcogramma*)			14	3.4			17[a]	4.9						
Saffron cod (*Eleginus gracilis*)			12	2.9										
Pacific cod (*Gadus macrocephalus*)									9	6.0				
Atka mackerel (*Pleurogrammus monopterygius*)	4	6.3												
Pacific sandfish (*Trichodon trichodon*)									1	0.7	11	3.1	1	1.5
Chum salmon (*Oncorhynchus keta*)							2	0.5						
Sockeye salmon (*O. nerka*)											5	1.6		
Prowfish (*Zaprora silenus*)	1	1.6			2	1.8							2	3.1
Kelp greenling (*Hexagrammos decagrammus*)									4	3.0				
Yellow Irish lord (*Hemilepidotus jordani*)	13	20.6												
Aleutian alligatorfish (*Aspidophoroides bartoni*)	1	1.6												
Lumpenus sp.			1	0.2										
Sebastes sp.			1	0.2										
Squid (Gonatidae)	21	33.3			4	3.6			4	3.0	1	0.3	10	15.4
Octopus (Octopodidae)							1	0.3			2	0.6	13	20.0
Crustacea			8	1.9										
Source	this study		this study		Manuwal and Boersma (1977)		this study		Manuwal and Boersma (1977)		Baird and Moe (1978)		Hatch et al. (1979)	

[a] Walleye pollack and saffron cod combined.

TABLE 2. Number and percent occurrence of prey in bill loads delivered by Tufted Puffins on Ugaiushak Island, 1976 and 1977.

	1976						1977					
	Early August		Late August		Total		Early August		Late August		Total	
Prey species	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
Pacific sand lance	319	88.8	51	87.9	370	88.8	249	92.6	38	46.9	287	82.0
Capelin	10	2.8	1	1.7	11	2.6	13	4.8	29	35.8	42	12.0
Gadids	20	5.6	6	10.4	26	6.2	3	1.1	14	17.3	17	4.9
Other	10	2.8	0	0.0	10	2.4	4	1.5	0	0.0	4	1.1
Total	359	100.0	58	100.0	417	100.0	269	100.0	81	100.0	350	100.0

Food delivery by Tufted and Horned puffins was similar to that of Atlantic Puffins (Myrberget 1962, Corkhill 1973), except that in over a dozen instances of food delivery to nestlings (both species combined) less than one week old, I never saw chicks take food directly from their parent's bill.

FEEDING FREQUENCY

Tufted Puffin chicks on Ugaiushak received from none to at least four loads of food daily; occasionally, some chicks were not fed for two consecutive days.

Parental feeding of Tufted and Horned puffin chicks was loosely synchronized within a population. Daily feeding activity began at sunrise and tended to occur in peaks every 1–2 h throughout the day, with most food deliveries made in the morning. On Buldir, over 60% of all deliveries occurred between sunrise (approximately 07:00) and 13:00, with less than 3% occurring between 19:00 and sunset (approximately 22:00) (Fig. 2).

On Buldir, the proportion of food-carrying adults to non-food-carrying adults observed during all-day watches on 12 and 22 August was similar for Tufted Puffins (12 Aug. = 3.2%, n = 1,338; 22 Aug. = 2.3%, n = 1,608; χ^2 = 2.18, $P > 0.05$) but decreased significantly for Horned Puffins (12 Aug. = 5.6%, n = 3,154; 22 Aug. = 2.2%, n = 5,821; χ^2 = 65.39, $P <$ 0.001).

Weather appeared to affect feeding activity only slightly. Even under the worst conditions (i.e., heavy rain and fog, waves over 2 m, or winds in excess of 80 km/h), some adults delivered food.

Other studies have found that Tufted and Horned puffins generally receive from two to four feedings daily, with a range of none to six for Tufted Puffins and two to six for Horned Puffins (Manuwal and Boersma 1977, Vermeer et al. 1979). The mean number of daily feedings for Atlantic Puffins during various colony years ranges from 2.3 to 15.0, with a maximum of 24 bill loads delivered to a single burrow in one day (Harris and Hislop 1978).

The lack of parental feeding for one or two days has been noted elsewhere for Tufted Puffins (Baird and Moe 1978, Vermeer et al. 1979), but has never been reported for Horned Puffins. During the nestling period, Tufted Puffins forage in inshore, offshore, and oceanic waters, depending on colony location, while Horned Puffins feed primarily in inshore waters (Wehle 1982). Seabirds that feed farther offshore tend to have longer intervals between feeding visits to their young than do species that forage closer to shore (Lack 1968).

My data on the relative proportions of Tufted and Horned puffins carrying food on 12 and 22 August were in variance with the tendency for puffins to increase the number of daily food deliveries during the period of peak nestling growth (Corkhill 1973, Ashcroft 1977, Manuwal and Boersma 1977, Harris and Hislop 1978).

PREY SPECIES COMPOSITION OF FOOD LOADS

In food loads of Tufted Puffins on Ugaiushak in 1976 and 1977, sand lance comprised over 80% of all prey items (Table 1). In 1976, most other prey consisted of nearly equal numbers of capelin and gadids (walleye pollock and saffron cod); in 1977, capelin accounted for two-thirds of all other prey. The relative proportions of sand lance, capelin, and gadids in early versus late August loads were similar in 1976 (χ^2 = 2.91, df = 2, $P > 0.05$), but differed significantly in 1977 (χ^2 = 98.28, df = 2, $P <$ 0.0001) when more capelin were taken later in the month (Table 2). The relative proportions of these three prey groups for the whole month were significantly different between the two years (χ^2 = 26.23, df = 2, $P < 0.0001$), again, largely because of the variation in numbers of capelin taken. On Buldir, sand lance and squid each comprised approximately 35% of all prey in Tufted Puffin bill loads, with the remaining prey consisting primarily of sculpin and Atka mackerel (Table 1).

In food loads of Horned Puffins on Ugaiushak, sand lance appeared to be the most nu-

TABLE 3. Number and percent occurrence of prey in bill loads delivered by Horned Puffins during various Alaskan colony years. See Table 1 for scientific names of prey species.

Prey species	Buldir Island 1975		Shumagin Islands 1976		Barren Islands 1976		Barren Islands 1977	
	No.	%	No.	%	No.	%	No.	%
Pacific sand lance	22	42.3	107	66.5	3	15.8	30	51.7
Capelin			34	21.1	14	73.7	26	44.8
Atka mackerel	22	42.3						
Pacific cod			17	10.6			1	1.7
Pacific sandfish			1	0.6	1	5.2	1	1.7
Whitespotted greenling (*Hexagrammos stelleri*)					1	5.2		
Yellow Irish lord	1	1.9						
Unidentified fish			2	1.2				
Squid (Gonatidae)	7	13.5						
Source	this study		Moe and Day (1979)		Manuwal and Boersma (1977)		Manuwal and Boersma (1977)	

merous prey in both years, with the remainder of prey being capelin and gadids. On Buldir, sand lance and Atka mackerel each accounted for about 42% of all prey; most of the remaining prey were squid (Table 3).

In other OCSEAP studies, the predominant prey species in Tufted and Horned puffin bill loads in all colony years were either sand lance or capelin (Tables 1 and 3); on Chowiet Island in 1976, sand lance were the predominant prey in 12 Tufted Puffin and 20 Horned Puffin loads (Leschner and Burrell 1977; G. Burrell, pers. comm.). Of 13 colony years for Tufted and Horned puffins in Alaska (Chowiet plus those given in Tables 1 and 3), 11 of them showed sand lance and/or capelin accounting for at least 85% of all prey, while for both species on Buldir, they accounted for less than 45% of all prey. Although sand lance and capelin were the primary prey species in both Tufted and Horned puffin bill loads, the composition of subordinate prey differed between puffin species. The most numerous lesser prey were (in decreasing order of abundance) for Tufted Puffins: cephalopods, gadids, sculpin, and greenling; and for Horned Puffins: greenling and gadids, squid, and sandfish (Tables 1 and 3).

Seasonal variation in prey species composition of bill loads has been noted for Tufted Puffins at Sitkalidak Strait (Baird and Moe 1978) and for Horned Puffins on the Shumagin Islands (Moe and Day 1979); in both colony years the occurrence of capelin in food loads decreased over the nestling period.

Seasonal, annual, and/or geographic variation in the prey species composition of bill loads occurs for Tufted Puffins in British Columbia (Vermeer 1979, Vermeer et al. 1979) and for Atlantic Puffins in Britain (Harris and Hislop 1978). Variation may result from differences in the availability or abundance of prey species, in the selection of specific prey by the puffins, or both. The cause of variation can best be determined by sampling the waters within the puffins' foraging range and concurrently analyzing the prey species composition of food loads. In Britain, the composition of North Sea trawl catches broadly resembles the composition of food loads of nearby Atlantic Puffins (Harris and Hislop 1978). This study also found that puffins tend to select more nutritious, but apparently less abundant, prey species. Coupled with the need for a similar study in Alaska is the need for greater knowledge of the life histories of puffin prey species in Alaskan waters. With the exception of the commercially exploited gadids, life history parameters of puffin prey are poorly understood.

PREY SIZE

Individual prey in Tufted and Horned puffin food loads were generally 50–100 mm long (Table 4). Tufted Puffin loads contained significantly smaller sand lance on Ugaiushak in 1976 than in 1977, or on Buldir in 1975; during both years on Ugaiushak, sand lance were significantly larger in late versus early August. Capelin in Tufted Puffin loads were also significantly smaller on Ugaiushak in 1976 than they were in 1977.

Tufted and Horned puffins on Buldir delivered nearly the same size sand lance, but Tufted Puffins delivered significantly larger squid than did Horned Puffins (Table 4).

Based on the relationship between sand lance body length and age class (Blackburn 1979), most sand lance in puffin bill loads were probably age classes 0 and 1 fish, with few fish in age class 2 present. Most capelin taken were probably age class 1 fish, with a few age class 0 and 2 fish present (Jangaard 1974). All squid in bill loads were probably subadults (Berry 1912, Roper and Young 1975). Seasonal variation in prey size may reflect either the summer growth of the fish or predation on different populations of fish as they move into the birds' foraging areas (Blackburn 1979) rather than the birds' selection of progressively larger fish.

The sizes of sand lance and capelin I found in Tufted and Horned puffin food loads are similar to those reported for other colony years (Hatch et al. 1979, Moe and Day 1979, Vermeer 1979), with the exception of Triangle Island, B.C., in 1978; there, Tufted Puffins delivered mostly age class 2 sand lance (Vermeer 1979). Seasonal and annual variations in the length of prey have been noted elsewhere for Tufted Puffins (Cody 1973, Baird and Moe 1978, Hatch et al. 1979, Vermeer 1979) and for Atlantic Puffins (Myberget 1962, Corkhill 1973, Harris and Hislop 1978).

SIZE AND WEIGHT OF FOOD LOADS

Tufted Puffins delivered significantly more prey per load on Ugaiushak in 1976 than in 1977, or on Buldir (Table 5). The size of loads was similar between early and late August in 1976, but decreased significantly during August in 1977. Tufted Puffin loads were significantly heavier on Ugaiushak in 1977 than in 1976, and were similar between early and late August within each year (Table 5).

Tufted and Horned puffins on Buldir delivered loads of similar size and weight (Table 5).

Means of both size and weight of food loads in this study fall within the ranges of those observed elsewhere in Alaska (Table 6). In other colony years where the loads of Tufted and Horned puffins were weighed, the weights did not differ significantly between species (Manuwal and Boersma 1977, G. Burrell, pers. comm.). Although seasonal and annual variation in load size and weight have been reported for Tufted Puffins at other colonies (Cody 1973, Manuwal and Boersma 1977, Baird and Moe 1978, Vermeer et al. 1979), the statistical significance of the observed differences is unknown. Among Atlantic Puffins, the size of loads varies (Myrberget 1962, Corkhill 1973, Harris and Hislop 1978), whereas the weight of loads is generally similar between years and throughout the season at the same colony (Harris and Hislop 1978).

GROWTH RATES

Growth rates of Tufted and Horned puffin nestlings raised under various conditions on Buldir and Ugaiushak are given in Table 7. Unfed Tufted Puffin single chicks on Ugaiushak grew at the same rate in 1976 as in 1977, and significantly faster on Ugaiushak both years

TABLE 4. Length (mm) of individual prey of major prey species delivered by Tufted (TP) and Horned (HP) puffins on Buldir Island, 1975, and Ugaiushak Island, 1976 and 1977.

			Sand lance				Capelin				Squid				Atka mackerel		
Location	Time	Puffin species	n	Median	Range	Significance	n	Median	Range	Significance	n	Median	Range	Significance	n	Median	Range
Buldir	1975	TP	12	72.8	36–178	*					10	98.0	84–105	W = 121			
		HP	18	79.0	56–164	NS					7	64.5	30–94	$P < 0.005$	20	83.0	69–115
Ugaiushak	1976																
	early Aug.	TP	296	61.0	46–127	W = 48449											
	late Aug.	TP	50	65.5	55–95	$P < 0.0001$											
	combined	TP	346	62.0	46–127	*	10	64.0	40–78	**							
	1977																
	early Aug.	TP	86	78.0	60–117	W = 4785	7	125.0	85–140	W = 149							
	late Aug.	TP	38	82.0	69–96	$P < 0.005$	21	87.0	82–132	$P < 0.05$							
	combined	TP	124	79.0	60–117	*	28	87.0	82–140	**							

NS = not significant at $P \leq 0.05$.
* Difference among colony years: $H = 169.8$, df = 2, $P < 0.0001$; 1975 vs. 1976, experimental-wise $P < 0.05$; 1975 vs. 1977, NS ; 1976 vs. 1977, experimental-wise $P < 0.05$.
** W = 55.0, df = 1, $P < 0.0001$.

TABLE 5. Size and weight of bill loads delivered by Tufted (TP) and Horned (HP) puffins on Buldir Island, 1975, and Ugaiushak Island, 1976 and 1977.

Location	Time	Puffin species	Size (no. prey) *n*	Median	Range	Significance	Weight (g) *n*	Median	Range	Significance
Buldir	1975	TP	15	3.0	1–29	*	13	10.0	4.9–24.5	**
		HP	15	2.0	1–11	W = 244, NS	15	11.0	5.5–15.5	W = 184, NS
Ugaiushak	1976									
	early Aug.	TP	30	8.5	1–25	W = 663, NS	30	9.0	2.5–22.0	W = 608, NS
	late Aug.	TP	11	8.0	1–13		11	11.0	3.0–28.0	
	combined	TP	41	8.0	1–25	*	41	9.0	2.5–28.0	**
Ugaiushak	1977									
	early Aug.	TP	43	6.0	1–13	W = 154	15	13.5	7.0–34.0	W = 202, NS
	late Aug.	TP	21	5.0	1–9	$P < 0.05$	16	15.5	5.0–22.5	
	combined	TP	64	6.0	1–13	*	31	14.0	5.0–34.0	**

NS = not significant at $P \leq 0.05$.
* Difference among colony years: $H = 13.2$, df = 2, $P < 0.005$; 1975 vs. 1976, experimental-wise $P < 0.05$; 1975 vs. 1977, NS; 1976 vs. 1977, experimental-wise $P < 0.05$.
** Difference among colony years: $H = 18.8$, df = 2, $P < 0.001$; 1975 vs. 1976, NS; 1975 vs. 1977, NS; 1976 vs. 1977, experimental-wise $P < 0.05$.

than on Buldir ($H = 6.11$, df = 2, $P < 0.05$; experimental-wise $P < 0.01$). The growth rates of unfed and fed Tufted Puffin singles and twins in 1977 did not differ significantly among the four groups ($H = 5.48$, df = 3, $P > 0.05$).

Unfed Horned Puffin singles also grew significantly faster on Ugaiushak in 1977 than those on Buldir (W = 3.00, $P < 0.05$). Growth rates did not differ significantly among Horned Puffin unfed and fed singles and unfed twins on Ugaiushak in 1977 ($H = 4.14$, df = 2, $P > 0.05$).

The similar growth rates among the four groups of Tufted Puffins in 1977 suggest that adults of unfed nestlings were delivering close to the maximum amount of food the chicks could use. During my daily feeding of fed nestlings, I never saw uneaten food in the nest. Because the fed chicks grew as rapidly as unfed chicks, the adults apparently compensated for my food supplements by delivering less food themselves. This would be expected if feedback exists between chicks and adults, as has been observed in Pied Flycatchers (*Ficedula hypoleuca*; von Haartman 1949).

Among various colony years in Alaska, the growth rate (K) of Tufted Puffins varied by 107% and Horned Puffins by 92% (Table 8).

TABLE 6. Size and weight of bill loads delivered by Tufted and Horned puffins during various Alaskan colony years (n = number of bill loads).

Species Year	Location	Weight *n*	$\bar{x}$	SD	Range	Size *n*	$\bar{x}$	SD	Range	Source
Tufted Puffin										
1975	Buldir Island	13	11.9	6.2	5.0–24.5	15	4.3	4.1	1–29	this study
1976	Ugaiushak Island	41	9.7	6.1	2.5–28.0	41	9.4	5.5	1–22	this study
	Barren Islands	24	14.9	—	2.0–36.5	79	3.8	—	1–8	Manuwal and Boersma (1977)
	Chowiet Island	12	7.5	3.6	2.3–16.8	12	10.1	4.2	1–15	G. Burrell (pers. comm.)
1977	Ugaiushak Island	31	14.4	5.2	5.0–34.0	64	5.6	3.4	1–13	this study
	Barren Islands	28	20.4	—	9.0–35.0	58	3.4	—	1–8	Manuwal and Boersma (1977)
	Sitkalidak Strait	10	19.3	6.2	13.5–35.0	—	—	—	—	R. A. Moe (pers. comm.)
Horned Puffin										
1975	Buldir Island	15	11.0	3.3	5.5–15.7	15	3.5	3.1	1–11	this study
1976	Barren Islands	9	10.7	—	3.0–19.0	26	1.5	—	1–3	Manuwal and Boersma (1977)
	Chowiet Island	19	7.9	4.4	2.5–19.0	19	12.6	14.5	2–65	G. Burrell (pers. comm.)
	Shumagin Islands	18	13.8	3.9	7.4–25.4	18	6.0	4.7	1–16	Moe and Day (1979)
1977	Barren Islands	13	17.0	—	3.0–35.0	20	3.2	—	1–7	Manuwal and Boersma (1977)

TABLE 7. Growth rates of Tufted and Horned puffin chicks reared under various conditions on Buldir Island, 1975, and Ugaiushak Island, 1976 and 1977.

			Tufted Puffin		Horned Puffin	
Location	Year	Condition	n	Median growth rate (g/day)	n	Median growth rate (g/day)
Buldir	1975	unfed singles	2	5.2	2	4.9
Ugaiushak	1976	unfed singles	27	15.7	—	—
		unfed twins	1[a]	7.5	—	—
	1977	unfed singles	10	15.9	10	10.9
		fed singles	5	16.2	4	10.9
		captive singles	1	17.2	2	8.9
		unfed twins	3	14.2	3	7.8
		fed twins	7	14.6	—	—
		captive twins	—	—	1	9.0

[a] For twins, *n* is the number of twinned pairs.

However, most of this variation was attributed to the much slower growth rates of Tufted Puffins on Buldir and Chowiet islands and for Horned Puffins on Buldir than in all other colony years. Excluding Buldir and Chowiet, *K* values for Tufted and Horned puffins varied by only 39% and 27%, respectively.

FLEDGING SUCCESS

Few Tufted or Horned puffin chicks fledged before I left Ugaiushak in 1976 or 1977 (Table 9). All observed nestling mortality during these years occurred among chicks less than two weeks old. The most commonly reported causes of death in chicks older than that are predation by terrestrial predators (Amaral 1977; Mickelson et al. 1977, 1978) and insufficient food (Vermeer et al. 1979). In the absence of terrestrial predators on Ugaiushak and because of the unfed chicks' comparatively high growth rates (Tables 7 and 8), I suspect that all unfed single chicks fledged after my departure.

No experimental chicks fledged in either year on Ugaiushak before I left. Of 28 sets of non-captive chicks twinned, one chick in each of 14 sets either disappeared or died (being rejected by the adults or forcibly kept from food by its nest-mate); all other chicks were alive when I left the island. Except for the one set of unfed Tufted Puffin twins in 1976, growth rates of non-captive experimental birds compared favorably with those of unfed single chicks (Table 7); consequently, I assume that all of these chicks eventually fledged. In 1977, I found the banded remains of one of the unfed Tufted Puffin twins of 1976 in its burrow; the fate of the other chick is unknown.

On Buldir in 1975, I found only three young

TABLE 8. Specific growth parameters of Tufted and Horned puffins during various Alaskan colony years.[a]

						Growth rate	
Year	Location	n	Asymptote (g)	Adult weight (g)	$R = a/W$	K	$(KR/4) \times 100$ (%/day)
Tufted Puffin							
1975	Buldir Island	2	360	755	0.48	0.074	0.9
1976	Ugaiushak Island	27	600	792	0.76	0.125	2.4
	Barren Islands	12	600	784	0.77	0.111	2.1
	Chowiet Island	12	330	780	0.42	0.091	1.0
	Shumagin Islands	15	520	830	0.63	0.145	2.3
	Wooded Islands	2	550	792[b]	0.69	0.120	2.1
1977	Ugaiushak Island	10	555	792	0.70	0.153	2.7
	Barren Islands	23	595	784	0.76	0.110	2.1
	Sitkalidak Strait	10	590	792[b]	0.75	0.126	2.4
	Cathedral Island	24	580	792[b]	0.73	0.127	2.3
Horned Puffin							
1975	Buldir Island	2	300	491	0.61	0.075	1.2
1976	Barren Islands	3	440	600	0.73	0.122	2.2
	Chowiet Island	12	280	519	0.54	0.113	1.5
	Shumagin Islands	9	405	549	0.74	0.144	2.6
1977	Ugaiushak Island	10	380	526	0.72	0.139	2.5
	Barren Islands	7	445	600	0.74	0.114	2.1

[a] Growth parameters were calculated from data supplied by OCSEAP investigators at each colony (see introduction and other tables), except for the Barren Islands which are given in Manuwal and Boersma (1977). Cathedral Island data were provided by R. A. Moe (pers. comm.).
[b] Mean adult weight of Tufted Puffins on Ugaiushak Island.

TABLE 9. Estimated fledging success, fledging weight, and weight of nestlings not fledged by last check[a] for unfed single Tufted and Horned puffins on Ugaiushak Island, 1976 and 1977.

	Tufted Puffin						Horned Puffin		
	1976			1977			1977		
	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD
Total number of nestlings monitored	50			21			11		
Nestlings fledged	19 (38%)	567	37.2	6 (29%)	556	37.3	0		
Nestlings of fledging weight[b] not fledged	21 (42%)	563	36.6	7 (33%)	572	44.8	1 (9%)	403	
Nestlings below fledging weight not fledged	3 (6%)	469	35.5	7 (33%)	385	64.5	9 (82%)	328	59.2
Known nestling mortality	7 (14%)			1 (5%)			1 (9%)		
Estimated fledging success	86%			95%			91%		

[a] 1976 = 2 September; 1977 = 27–28 August.
[b] Tufted Puffin = 496 g; Horned Puffin = 400 g.

each of Tufted and Horned puffins. Of these, one chick of each species had been deserted by its parents. None of the four remaining chicks, ranging in age from 42 to 46 days, had fledged when I left the island. All four chicks grew much more slowly than chicks in other colony years (Table 8) and when last weighed were at least one-third lighter than chicks of equivalent ages on Ugaiushak in 1976 and 1977. Because of their very slow growth rates, I doubt that any of these chicks fledged.

Estimates of fledging success on Ugaiushak for Tufted Puffins in 1976 and 1977 and for Horned Puffins in 1977 were the highest reported for any colonies during those years (Table 10). Breeding failures comparable to those suspected for Tufted and Horned puffins on Buldir and thought to be related to poor feeding conditions have been reported for Tufted Puffins on Triangle Island, British Columbia (Vermeer et al. 1979) and for Atlantic Puffins in Britain, Norway, and Newfoundland (Boddington 1960, Mills 1981, Working Group on Atlantic Seabirds 1982).

Aspects of food delivery are primarily inherent characteristics of puffin feeding behavior, presumably not subject to variation in response to environmental change. Other components of nestling ecology may, however, be affected, and thus may serve to indicate changes in feeding conditions. Of these, fledging success is overall the best measure of a population's reproductive health, but it is often affected by factors other than feeding conditions (e.g., weather [Manuwal and Boersma 1977], predation [Amaral 1977, Lehnhausen 1980]). Growth rate, on the other hand, is sensitive to variations in feeding conditions (Ricklefs and White 1975) and is largely determined by the combined effects of feeding frequency, prey size, and the prey species composition, size, and weight of food loads.

My interpretation that slow growth in Tufted and Horned puffin chicks on Buldir was associated with poor feeding conditions in that year is based on three points. First, despite extensive searching, I found few chicks; many adults had apparently deserted their eggs or chicks early in the nestling period. A similar desertion by Tufted Puffins during incubation on Triangle Island may have been caused by food shortage or weather interference with foraging (Vermeer 1978). Second, contrary to an expected increase in numbers of adult puffins observed carrying food to their young on 12 versus 22 August, I saw no change in the number of Tufted Puffins and proportionally fewer Horned Puffins. A decrease in feeding frequency was associated with apparent food shortage and the starvation of young Atlantic Puffins (Harris and Hislop 1978). Third, capelin were absent and sand lance comprised less than 45% of all prey in puffin food loads on Buldir; in other colony years, where chicks also grew faster, sand lance and/or capelin made up at least 85% of all prey. The presence of specific prey species in Atlantic Puffin food loads resulted in significant differences in fledging weight (Harris and Hislop 1978). The slow growth rates of Tufted and Horned puffin chicks on Chowiet Island were also associated with poor feeding conditions, as indicated by 10% of the 48 chicks monitored having died of starvation (Leschner and Burrell 1977).

The growth rates of Tufted and Horned puffins on Buldir and Chowiet islands (0.9 to 1.5% of adult weight/day) provide data on rates of nestling growth during years when feeding conditions were apparently poor. Data on growth rates of chicks raised under apparently favorable feeding conditions are provided by the experimental chicks on Ugaiushak in 1977. Growth rates of Tufted Puffin unfed and fed singles and twins and Horned Puffin unfed and fed singles and unfed twins did not differ intraspecifically. These results indicate that

TABLE 10. Estimated fledging success of Tufted and Horned puffins during various Alaskan colony years (n = number of chicks monitored).

Year	Location	Tufted Puffin n	Tufted Puffin Fledging success (%)	Horned Puffin n	Horned Puffin Fledging success (%)	Source
1975	Buldir Island	2	0	2	0	this study
1976	Ugaiushak Island	50	86	—	—	this study
	Barren Islands	16	69	11	36	Manuwal and Boersma (1977)
	Chowiet Island	16	56	32	60	Leschner and Burrell (1977)
	Shumagin Islands	32	84	10	90	Moe and Day (1979)
1977	Ugaiushak Island	21	95	11	91	this study
	Barren Islands	39	79	13	69	Manuwal and Boersma (1977)
	Sitkalidak Strait	41	88	—	—	Baird and Moe (1978)
	Wooded Islands	93[a]	0	—	—	Lehnhausen (1980)

[a] Number of burrows monitored.

weight gains of 2.5% adult body weight/day were near maximum and that feeding conditions were nearly optimal. Although sample sizes were too small for statistical comparison, my interpretation is supported by the fact that captive chicks and unfed singles grew at similar rates. The data also suggest that a feedback mechanism in food delivery may exist between chicks and adults for both puffin species.

Data on the major components of the feeding ecology of nestling Tufted and Horned puffins for various colony years in Alaska are summarized in Table 11. They are insufficient to establish a reliable correlation between feeding conditions and feeding frequency, prey size, or prey species composition, size, and weight of food loads. Nevertheless, changes in feeding conditions should at least be suspected if data in future studies differ significantly from those presented in Table 11. Currently, however, growth rate alone is the most reliable criterion by which feeding conditions can be assessed.

The high growth rates and estimated fledging success of unfed Tufted and Horned puffin twins on Ugaiushak in 1977 neither refute nor support Lack's (1954) hypothesis that the clutch size of a bird species corresponds with the largest number of young for which the parents can, on the average, provide enough food. In addition, my findings do not strengthen or contradict Nelson's (1964) conclusion that, although some uniparous seabirds can rear two young sufficiently well to give those birds a substantial reproductive advantage over pairs having single chicks, they do not do so naturally. Although both Tufted and Horned puffin pairs were apparently able to fledge two young during that colony year, the data are too few to determine whether or not they could do so "on the average." In exception to Lack's (1954) view, the clutch size of many species of birds is determined by constraints on the laying female rather than the inability of pairs to feed more young (see Klomp 1970, von Haartman 1971).

That uniparity in puffins may be a result of such constraints is suggested by the results of egg replacement experiments I conducted on Ugaiushak in 1977 (Wehle 1980). In 10 each of Tufted and Horned puffin nests from which I removed the original egg soon after it was laid, 7 and 3 nests, respectively, contained a replacement egg 10–21 days later. Only if a female was able to lay a second egg soon after the first egg was lost (within several days rather than 10–21 days) could constraints on the laying female be discounted.

For the data to support Nelson's (1964) contention that pairs rearing two chicks had a substantial reproductive advantage over pairs with single chicks, several questions must be considered: (1) Is sufficient hardship imposed on the female by laying a second egg or on the pair by rearing two chicks to reduce their potential contribution of young? (2) Is post-fledging survival of two chicks less than that of singles? (3) Does the attempt to rear two chicks lower fledging success? No information is available on puffins to answer the first two questions, and current data are insufficient to answer the third (Nettleship 1972; Corkhill 1973; M. P. Harris, pers. comm.; this study).

CONCLUSIONS

Pacific sand lance and capelin are the most important prey species for nestling Tufted and Horned puffins in Alaska. More information is needed on the life histories of these fish in Alaskan waters and on the relationship between certain aspects of their life histories (e.g., age, size, seasonal movements) and predation by puffins and other seabirds.

Data for some aspects of the feeding ecology of nestling Tufted and Horned puffins currently are too variable to make a reliable correlation with feeding conditions. The data suggest that feeding frequency and prey species composition of food loads may be better indicators of feeding conditions than prey size

TABLE 11. Summarized data for major components of the feeding ecology of nestling Tufted and Horned puffins during various Alaskan colony years.

Component of feeding ecology	Tufted Puffin	Horned Puffin
Food delivery	—begins when chicks are one day old	—as for Tufted Puffin
	—food dropped on nest site floor, often near entrance	—as for Tufted Puffin
	—specific feeding behavior of adults, particularly when chicks are young	—as for Tufted Puffin
	—feedback mechanism may exist between chick behavior and stimulation of adults to deliver food	—as for Tufted Puffin
Feeding frequency	—0–6 food loads/day, chicks sometimes not fed for two consecutive days	—2–6 loads/day
	—loosely synchronized within population	—as for Tufted Puffin
	—throughout daylight hours, most deliveries in morning	—as for Tufted Puffin
Variation[a]	—seasonal, tending to increase with chick age (?)	—unknown
Prey species		
Primary prey	—sand lance and capelin	—as for Tufted Puffin
Subordinate prey	—cephalopods, gadids, sculpin, greenling	—greenling, gadids, cephalopods, sandfish
Variation	—seasonal, annual, geographic	—as for Tufted Puffin
Prey size/Age	—usually 50–100 mm	—as for Tufted Puffin
	—sand lance mostly age classes 0 and 1 fewer age class 2; capelin mostly age class 1, fewer age classes 0 and 2; squid all subadults	—sand lance and squid as for Tufted Puffin
Variation	—seasonal (no trend), annual, geographic	—unknown
Bill load size (no. prey)		
$\bar{x} \pm$ SD, n' (n'')[b]	—5.3 ± 2.3, 6 (269)	—5.2 ± 4.0, 5 (98)
Range of n' (n'')	—3.4–10.1 (1–29)	—1.5–12.6 (1–65)
Variation	—seasonal (no trend), annual, geographic (?)	—annual (?), geographic (?)
Bill load weight (g)		
$\bar{x} \pm$ SD, n' (n'')	—13.9 ± 4.3, 7 (159)	—11.9 ± 3.2, 5 (74)
Range of n' (n'')	—7.5–20.4 (2.3–36.5)	—7.9–17.0 (2.5–35.0)
Variation	—annual, geographic (?)	—geographic (?)
Growth rates (%/day)		
$\bar{x} \pm$ SD, n' (n'')	—2.2 ± 0.5, 10 (137)	—2.1 ± 0.5, 6 (43)
Range of n'	—0.9–2.7	—1.2–2.7
Variation	—geographic	—as for Tufted Puffin
Fledging success[c] (%)		
$\bar{x} \pm$ SD, n' (n'')	—82 ± 11, 8 (217)	—65 ± 21, 6 (79)
Range	—0–95	—0–91
Variation	—annual (?), geographic (?)	—as for Tufted Puffin

[a] Seasonal variation is that observed during nestling period at same colony in same year; annual variation is that observed at same colony among years; geographic variation is that observed among colonies. Question marks indicate non-statistically documented variation.
[b] Weighted mean and standard deviation for all colony years combined; n' is number of colony years; n'' is total number of samples for all colony years combined.
[c] Percent of chicks hatched.

or load size and weight. Nevertheless, growth rate (as the combined product of all components) is currently the best indicator of feeding conditions for puffins. Growth rates of 1.5% adult body weight/day or less reflect poor feeding conditions and, in general, are correlated with low fledging success; growth rates of 2.5% or more reflect the best feeding conditions and, in the absence of other mortality factors, are associated with high fledging success. Growth rates have varied considerably among colony years in studies thus far. Hence, data from a number of colony years will be needed in order to establish a credible relationship between offshore development and changes in feeding conditions as indicated by growth rates.

In years of favorable feeding conditions, pairs of both Tufted and Horned puffins can successfully rear two chicks; that they do not do so naturally is probably the result of constraints on the laying female.

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RECENT PUBLICATIONS

Handbook of the Birds of Europe, the Middle East, and North Africa/The Birds of the Western Palearctic. Volume III. Waders to Gulls.—Edited by Stanley Cramp with K. E. L. Simmons, Duncan J. Brooks, N. J. Collar, Euan Dunn, Robert Gillmor, P. A. D. Hollom, Robert Hudson, E. M. Nicholson, M. A. Ogilvie, P. J. S. Olney, C. S. Roselaar, K. H. Voous, D. I. M. Wallace, Jan Wattel, and M. G. Wilson. 1983. Oxford University Press, Oxford, London, and New York. 913 p. £ 49.50. This volume follows the same basic plan as its predecessors (noticed in Condor 80:253 and 83:141). Owing to the large number of charadriiform species in the region and the great deal that is known about them, it has been necessary to relegate the terns, skimmers, and alcids to the next volume, together with the remainder of the non-passerines. The treatment of certain topics has been revised to overcome problems that became manifest in the previous volumes and, more importantly, to adjust to the habits of the birds under consideration. The book is illustrated with 105 color plates as well as countless drawings, maps, sound spectrograms, and diagrams of the annual cycle. Staggeringly comprehensive, this superb reference work is essential for anyone working on charadriiforms, whether palearctic species or not. References, corrections to volumes I and II, and index.

Whistling-ducks: Zoogeography, Ecology, Anatomy.—Eric C. Bolen and Michael K. Rylander. 1983. Special Publications No. 20, The Museum, Texas Tech University. 67 p. Paper cover. $12.00. Source: Texas Tech Press, Sales Office, Texas Tech University Library, Lubbock, Texas. 79409. The eight species of *Dendrocygna* are distributed around the world, largely between the 30th parallels, north and south. This report collects published and unpublished information on them, principally from the authors' own previous papers. Distribution and zoogeography, comparative habits, and anatomy (chiefly skeletomuscular) are treated, concentrating on the four best-known species. A brief appendix tabulates the state of sixty morphological and life history characters for these same species and gives a phenogram based on these data. The report is useful as a compilation but it sheds little new light on the systematic position, ecology, or behavior of whistling-ducks. Their whistling is not mentioned. Maps, drawings, references.

Anatomy of the Domestic Birds.—R. Nickel, A. Schummer, and E. Seiferle. 1977. Verlag Paul Parey, Berlin and Hamburg. 202 p. Source: Springer-Verlag New York, 175 Fifth Ave., New York, NY 10010. This is a textbook on the anatomy of the fowl and other domestic birds, which has been skillfully translated from the German original edition (1973) by two British poultry anatomists, W. G. Siller and P. A. L. Wight. Conventional in plan and treatment, it marches through the organ systems from skeleton to skin. The approach is heavily descriptive and lightly, if at all, physiological or functional. The level of detail is mostly gross, with little attention paid to microanatomy. Many drawings (a few in color) are provided, the majority of them original; although well executed and reproduced, they show no new views. References, index. As a sound, convenient source of basic descriptive information, this book compares well with those by King and McLelland (noticed in Condor 78:148), T. Koch (*Anatomy of the Chicken and Domestic Birds.* 1973. Iowa State Univ. Press, Ames), and Schwarze and Schröder (noticed in Condor 82:9), yet each of these has certain advantages. For standardized terminology and more details, particularly on microanatomy and physiology, one must consult the works edited by Baumel (noticed in Condor 82:397) or King and McLelland (noticed in Condor 82:327, 84:21).