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FOOD HABITS OF THE WHISKERED AUKLET AT BULDIR ISLAND, ALASKA[1]

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Abstract. We studied the food habits of Whiskered Auklets (*Aethia pygmaea*) at Buldir Island, western Aleutian Islands, Alaska, during the summer of 1976. At Buldir, these birds fed primarily in and near convergent tidal fronts in the passes between three islets just offshore; feeding occurred throughout the day. Whiskered Auklets ate at least 10 different species of zooplanktonic prey, of which the copepod *Neocalanus plumchrus* was the most important. Next in importance were chaetognaths (probably *Sagitta elegans*), the amphipod *Parathemisto pacifica,* megalopae of the crab *Erimacrus isenbeckii,* and an unidentified amphipod. Pteropods (probably *Limacina helicina*), larval cephalopods, and a larval fish occurred in trace amounts. During most of the summer, Whiskered Auklets were nearly monophagous on *N. plumchrus*; we do not consider a difference in prey during late incubation/early chick rearing to represent a biologically-significant trend.

We collected Least (*A. pusilla*), Crested (*A. cristatella*), and Parakeet (*Cyclorrhynchus psittacula*) auklets during late chick rearing, to compare their food habits with those of Whiskered Auklets. At this time, both Least and Whiskered auklets were monophagous on smaller *N. plumchrus,* whereas Crested and Parakeet auklets mainly ate larger *N. cristatus* and *P. pacifica*; Parakeet Auklets ate the widest diversity of zooplankton. Selection of prey by the four auklet species appeared to occur in relation to size, with the smaller auklets eating smaller zooplankters.

Key words: Whiskered Auklet; food habits; oceanic zooplankton; tidal fronts; Least Auklet; Crested Auklet; Parakeet Auklet; competition.

INTRODUCTION

The Whiskered Auklet (*Aethia pygmaea*) is one of four plankton-feeding auklet species that are confined to the Bering Sea and the Sea of Okhotsk (AOU 1983). This species exhibits broad ecological overlap with the other three auklet species (Least Auklet, *A. pusilla*; Crested Auklet, *A. cristatella*; and Parakeet Auklet, *Cyclorrhynchus psittacula*) in nesting and in feeding: all generally nest in rock crevices and feed on zooplankton. The four species do differ in size, however, in that the smallest member of the group (Least Auklet) weighs only 84 g (SD = 7 g; range = 72–98 g; n = 457), whereas the largest members of the group (Crested Auklet and Parakeet Auklet) weigh 264 g (SD = 19 g; range = 195–330 g; n = 192) and 258 g (SD = 19 g; range = 215–292 g; n = 42), respectively (Knudtson and Byrd 1982; Day and Byrd, unpubl. data). The Whiskered Auklet, which weighs an average of 121 g (SD = 7 g; range = 102–138 g; n = 60), is slightly larger than the Least Auklet and considerably smaller than Crested and Parakeet auklets.

Although the four auklet species exhibit broad ecological overlap, these differences in size result in fine-scale partitioning of nesting habitat and food resources. For example, all four species nest in rock crevices (primarily in talus slopes), but the crevices used are of different sizes, with crevice size proportional to the size of the bird (e.g., Least Auklets use the smallest crevices, Crested Auklets use the largest; Bédard 1969c, Knudtson and Byrd 1982). Partitioning of food resources also has been observed for Least, Crested, and Parakeet auklets (Bédard 1969b, Hunt et al. 1981), but practically nothing has been published about the food habits of the Whiskered Auklet (Vermeer et al. 1987).

Bédard (1969a) predicted that the small difference in size between Least and Whiskered auklets should cause extensive overlap in food habits. He further suggested that this (hypothesized) competition caused the paucity of Whiskered Auklets in the Aleutian Islands, where Least

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Auklets are present, and the abundance of Whiskered Auklets in the Kuril Islands, where Least Auklets are absent. We thus conducted this study to describe the prey eaten by the Whiskered Auklet throughout its breeding season and to compare the foods of Whiskered Auklets with those of Least, Crested, and Parakeet auklets. The study was conducted at Buldir Island (52°24′N, 175°56′E), Alaska, where all four species of auklets breed (Knudtson and Byrd 1982, Byrd et al. 1983, Byrd and Day 1986).

METHODS

The at-sea distribution of Whiskered Auklets was studied in the vicinity of Buldir Island during May–August 1985 and 1986 (M. A. Spindler, U.S. Fish and Wildlife Service, unpubl. manuscript). Data were collected at a total of 269 seabird transect stations. These line transects were 300 m wide by a distance that was covered in either 10 min or 15 min of time while the boat was moving forward in a straight line at a known speed. Later, data were stratified into "nearshore" (<3 nm [5.5 km] from shore) and "offshore" (≥3 nm [5.5 km] from shore) transects. Thus, offshore transects occurred anywhere in the 70-nm-wide (130-km-wide) passes to the east and west of Buldir (Fig. 1).

We collected Whiskered Auklets at Buldir Island from a small boat during late egg laying/early incubation (26 May; six birds), late incubation/early chick rearing (1–2 July; six birds), and middle and late chick rearing (15–16 July; seven birds; and 4 August; six birds) in 1976; we also have included data from one bird collected on 3 August 1974. For comparison of food habits during the chick-rearing period in 1976, we collected four Parakeet Auklets (5 August), three Least Auklets (15 and 31 July), and seven Crested Auklets (5 August). All birds were collected within 1.0 km of the north shore of the island. Stomachs were preserved in buffered formalin and later were transferred to 10% isopropanol for sorting and identification.

In the laboratory, we sorted and identified all prey items in each stomach to the lowest possible taxon, counted the number of recognizable individuals of each taxon, and weighed the tissue of each taxon to the nearest 1 mg. When only fragments of a taxon were encountered, the number of individuals of that taxon was recorded as 1+, and the number used for that bird in the data summaries was 1. Percentages of total numbers and total weights that were <0.1% for a given taxon were rounded to 0.1% in the data summaries. Because of the small sample sizes of auklets, data from both sexes were combined for the data summaries. Data from stomachs and sublingual pouches also were combined, because the foods were essentially identical.

Food samples from five of the seven Crested Auklets were too large for analyses of each individual food item; these five stomachs contained an estimated 400–2,400 prey items. For these stomachs, we used a Stemple pipette (commonly used for subsampling zooplankton samples) to take two subsamples totaling 5.0–13.2% of the total volume of food items. Identifications, numbers, and weights were determined for these subsamples, then total numbers and weights of each taxon were estimated for each of the subsampled birds from the subsample data.

Only those birds containing food were considered in the data summaries; out of 40 auklets collected, only one had an empty stomach (a Whiskered Auklet on 16 July). For each taxon, we calculated the three frequently-reported measures of food habits: percent frequency of occurrence (F), percent of the total number of individuals of all taxa combined (N), and percent of the total weight of all taxa combined (W). We then calculated an Index of Relative Importance (IRI) with an equation modified from Pinkas (1971):

$$\text{IRI} = \text{F}(\text{N} + \text{W}).$$

IRI values range from 0.02 [i.e., 0.1% × (0.1% + 0.1%)] to 20,000 [i.e., 100% × (100% + 100%)], with larger numbers representing food items that are relatively "important" in the birds' diets. IRI values combine the three main attributes that frequently are discussed separately in feeding studies and thus provide an overall analysis of the relative importance of prey taxa.

RESULTS

FORAGING HABITAT

At Buldir Island, Whiskered Auklets fed primarily in and near convergent tidal fronts that formed in and near the passes between three islets just off the northwestern corner of the island (Fig. 1). All birds were collected in these tidal fronts, and 25 of 26 contained food. Whiskered Auklets apparently feed diurnally, for we encountered them during every visit to the tide rips

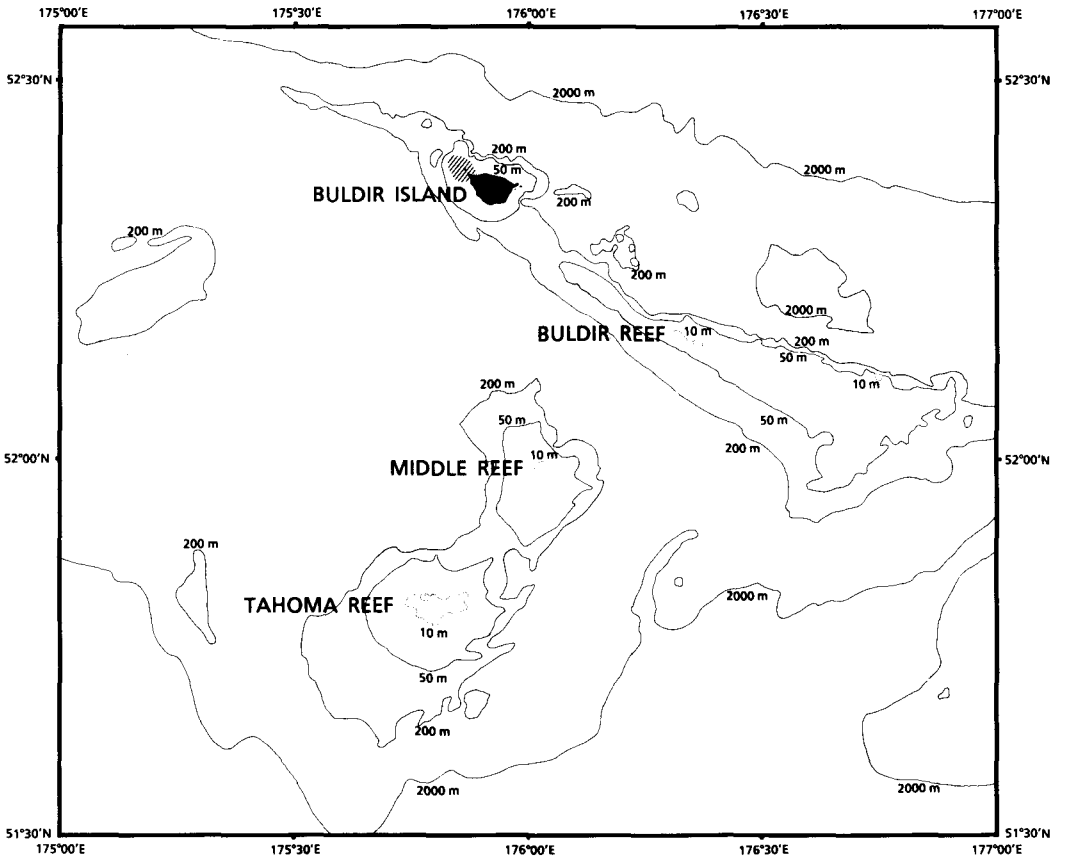

FIGURE 1. Bathymetry in the vicinity of Buldir Island, Alaska. Shading delineates the primary foraging area of Whiskered Auklets.

(09:00–22:00 local time); we did not determine if nocturnal feeding also occurs.

Whiskered Auklets were seen on nine (36.0%) of 25 seabird transects in nearshore (<5.5 km from shore) waters, but significantly fewer (χ^2 = 19.36; df = 1; $P < 0.001$) were seen in offshore (≥5.5 km from shore) waters around Buldir (19 [7.8%] of 244 transects; Spindler, unpubl.). Further, those records from offshore waters occurred only early in the breeding season, during May and June. We interpret these results to indicate that this species is primarily a nearshore feeder during the breeding season.

This pattern of feeding at tidal fronts, "tide rips," or standing waves also occurs elsewhere in the Aleutians. For example, Byrd and Gibson (1980) found most Whiskered Auklets near tide rips, usually within 16 km of land, during their surveys throughout the Aleutians. In the eastern Aleutians, Day and B. E. Lawhead estimated approximately 10,000 Whiskered Auklets feeding in standing waves 1–2 m high in Kagamil Strait (Islands of Four Mountains) on 2 June 1978, and G. A. Putney (pers. comm.) saw "thousands" the following day in tide rips between Amukta and Chagulak islands (Islands of Four Mountains). In the central Aleutians, E. P. Knudtson and Day saw approximately 200 birds feeding in tide rips off Ugidak Island (Delarof Islands) on 30–31 July 1977. In the western Aleutians, T. J. Early (U.S. Fish and Wildlife Service; pers. comm.) saw approximately 750 birds feeding in a tidal front off the southwestern corner of Kiska Island (Rat Islands) on 10 August 1978.

FOOD HABITS—GENERAL

Whiskered Auklets at Buldir ate prey of at least 10 species (Table 1). Zooplanktonic crustaceans

were the most important prey, with chaetognaths, molluscs, and larval fishes next in decreasing order of importance. Copepods formed a majority of the food, with *Neocalanus plumchrus* alone constituting at least 87.8% of the total IRI. In contrast, *N. cristatus* rarely was eaten by Whiskered Auklets (0.2% of total IRI), being recorded only twice. Chaetognaths were next in importance (0.2% of total IRI), with most individuals probably *Sagitta elegans* (the most common epipelagic chaetognath in this area—see Bieri 1959; Fager and McGowan 1963; Kotori 1976; Cooney 1981, 1987). The hyperiid amphipod *Parathemisto pacifica* and megalopae of the crab *Erimacrus isenbeckii* were recorded in trace amounts. Pteropods, probably *Limacina helicina* (the shells had dissolved; also see Fager and McGowan 1963; Cooney 1981, 1987), were the primary molluscan prey. Larval cephalopods and a larval fish were too fragmented to be identified.

FOOD HABITS—TEMPORAL TRENDS

In late May (late egg laying/early incubation of these birds; Knudtson and Byrd 1982), Whiskered Auklets were eating primarily *N. plumchrus* (62.0% of total IRI). An additional 36% of the total IRI consisted of copepod fragments, making copepods (probably all *N. plumchrus*) almost 98% of the total foods at this time. About 2% of the food consisted of unidentified chaetognaths, with crustacean fragments the remaining prey.

In early July (late incubation/early chick rearing), Whiskered Auklets appeared to have switched to eating a variety of foods. The amphipod *P. pacifica* was the dominant food (33.8% of total IRI), with *N. cristatus* second (30.1% of total IRI) and *N. plumchrus* third in importance (25.2% of total IRI). The remaining 11% consisted of copepod fragments, an unidentified amphipod, amphipod fragments, an unidentified chaetognath, crustacean fragments, and unidentified animal tissue. We doubt that this difference is biologically significant, however, because the amount of food in this sample of stomachs was relatively small: the number of individuals represented only 2.9% and the mass represented only 5.4% of the totals for the entire sample of stomachs. Hence, *P. pacifica* and *N. cristatus* were inflated in importance during this sampling period, whereas they clearly were unimportant during the summer as a whole (Table 1).

In mid-July (middle chick rearing), Whiskered Auklets again exhibited near-monophagy on *N. plumchrus* (88.1% of total IRI). A further 8.7% of the total IRI consisted of copepod fragments, probably of the same species. The remaining 3.2% of the food consisted of an unidentified euphausiid, megalopae of *E. isenbeckii,* crustacean fragments, and unidentified pteropods (probably *L. helicina*), cephalopods, and chaetognaths.

In early August (late chick rearing), Whiskered Auklets moved even closer to monophagy than they had been earlier. *Neocalanus plumchrus* constituted 90.4% of the total IRI, *N. cristatus* was present in trace amounts, and copepod fragments (probably *N. plumchrus*) formed another 9.3% of the total. Thus, 99.8% of the food consisted of copepods, with essentially all probably being *N. plumchrus.* The remaining 0.2% of the food consisted of unidentified chaetognaths, a larval fish, crustacean fragments, and animal tissue.

FOOD HABITS—THE AUKLETS COMPARED

Food habits of Least, Crested, and Parakeet auklets at Buldir are compared with those of Whiskered Auklets in Table 2. These data illustrate the major prey eaten by these zooplankton-feeders at Buldir.

Least Auklets fed primarily on *N. plumchrus,* with an unidentified amphipod, euphausiid fragments, and one pteropod (*L. helicina*) recorded in trace amounts. Crested Auklets fed primarily on *N. cristatus* and secondarily on *P. pacificus. Neocalanus plumchrus* were relatively unimportant, as were unidentified copepods and euphausiid and crustacean fragments. Parakeet Auklets ate a wider diversity of foods, with at least 11 taxa recorded from the four stomachs. *Neocalanus cristatus, P. pacifica,* and *E. isenbeckii* were the primary prey (in decreasing amounts). *Neocalanus plumchrus* constituted only 2% of the total, and the remaining prey consisted of a gammarid amphipod, the commensal hyperiid amphipod *Hyperia medusarum* (see Bédard 1969b), another hyperiid, *H. macropa,* euphausiids, shrimp larvae of two species, and an unidentified chaetognath.

At Buldir, *Neocalanus* copepods clearly were the primary food source of all four species of auklets (Table 2). The two smaller auklets took primarily the smaller *N. plumchrus,* whereas the two larger auklets took primarily the larger *N. cristatus.* In addition, the two larger auklet species ate significant amounts of the large *P. pacifica*

TABLE 1. Occurrence, number, weight of, and Index of Relative Importance (IRI) of prey of Whiskered Auklets at Buldir Island, Alaska, 26 May–4 August 1976 (n = 25 stomachs with food).

Taxon	Occurrence		Number		Weight		IRI	
	n	(%)	n	(%)	mg	(%)	Total	(%)
Arthropoda								
Copepoda								
Neocalanus plumchrus	19	(76.0)	2,765	(95.8)	7,090	(64.5)	12,182.8	(87.8)
N. cristatus	2	(8.0)	24	(0.8)	256	(2.3)	24.8	(0.2)
Copepod fragments	15	(60.0)	15	(0.5)	2,633	(24.0)	1,470.0	(10.6)
Amphipoda								
Parathemisto pacifica	1	(4.0)	38	(1.3)	192	(1.7)	12.0	(0.1)
Unidentified amphipod	2	(8.0)	2	(0.1)	2	(<0.1)	1.6	(0.1)
Amphipod fragments	1	(4.0)	1	(<0.1)	34	(0.3)	1.6	(<0.1)
Euphausiacea								
Unidentified euphausiid	1	(4.0)	1	(<0.1)	35	(0.3)	1.6	(<0.1)
Decapoda								
Erimacrus isenbeckii	1	(4.0)	2	(0.1)	35	(0.3)	1.6	(<0.1)
Unidentified crustacean fragments	6	(24.0)	6	(0.2)	598	(5.4)	134.4	(1.0)
Mollusca								
Gastropoda								
Unidentified pteropod	2	(8.0)	13	(0.5)	28	(0.2)	5.6	(<0.1)
Cephalopoda								
Unidentified cephalopod	2	(8.0)	5	(0.2)	5	(<0.1)	2.4	(<0.1)
Chaetognatha								
Unidentified chaetognath	8	(32.0)	10	(0.3)	77	(0.7)	32.0	(0.2)
Chordata								
Osteichthyes								
Unidentified fish	1	(4.0)	1	(<0.1)	3	(<0.1)	0.8	(<0.1)
Unidentified animal tissue	3	(12.0)	3	(0.1)	3	(<0.1)	2.4	(<0.1)
Total			2,886		10,991		13,873.6	

TABLE 2. Importance of selected prey taxa to four species of auklets at Buldir Island, Alaska, during late July/early August 1976. Values are expressed as percentages of the total Index of Relative Importance (IRI).

Taxon	Least Auklet	Whiskered Auklet	Crested Auklet	Parakeet Auklet
Arthropods				
Copepoda (total)[1]	86.6	99.8	65.8	58.2
Neocalanus plumchrus	86.6	90.4	1.4	2.0
N. cristatus	0	<0.1	64.3	56.2
Unidentified copepod fragments	0	9.3	0.1	0
Amphipoda (total)[1]	0.1	<0.1	33.4	23.2
Parathemisto pacifica	0	0	33.4	21.5
Euphausiacea (total)[1]	0.1	0	0.1	0.9
Decapoda (total)[1]	0	0	0	16.2
Caridea (total)[1]	0	0	0	2.8
Brachyura				
Erimacrus isenbeckii	0	0	0	13.4
Unidentified crustacean fragments	13.1	<0.1	0.7	3.1
Mollusca				
Gastropoda				
Pteropoda (total)[1]	0.1	0	0	0
Cephalopoda (total)[1]	0	0	0	0
Chaetognatha				
Chaetognatha (total)[1]	0	0.1	0	0.1

[1] Total values represent the sums of IRIs of species constituting that higher-level taxon (e.g., the IRI of total Copepoda is the sum of individual IRIs of all copepod species); they do not represent a new IRI calculated for all taxa together within that higher-level taxon.

and the large *E. isenbeckii.* Euphausiids, pteropods, cephalopods, and chaetognaths were eaten in trace amounts by all four species.

DISCUSSION

All available information indicates that the Whiskered Auklet is adapted for feeding in nearshore, convergent tidal fronts. For example, in wide island passes (e.g., Amchitka Pass) far from nesting islands, only single Whiskered Auklets are seen (Day and Byrd, pers. observ.). The preference of this species for feeding near shore apparently extends to the winter, for Stejneger (1885) commented on the number of birds seen just off the beach in the Commander Islands (U.S.S.R.) during December and January.

We believe that these convergent tidal fronts are the dominant force affecting the distribution and abundance of prey for auklets (especially Whiskered Auklets) around Buldir Island and elsewhere in the Aleutian Islands; further, these fronts are stable in space and highly repeatable in time (with each tidal cycle). In the Aleutians, twice-daily tides between the Pacific Ocean and the Bering Sea provide the energy for frontal formation and upwelling. These convergent fronts are generated by the rapid flow of large volumes of water through "bottlenecks" (i.e., passes between islands or in passes between small islets). For example, at a tidally-generated convergent front in the English Channel, Pingree et al. (1974) found concentrations of zooplanktonic crustaceans (copepods, euphausiids, caridean larvae, and decapod zoeae and megalopae) to be up to 75 times higher within the front than on either side of it. In addition, some fronts near Buldir are generated by the flow of water across topographic shallows or shoals (e.g., the reefs), also causing upwelling (Owen 1981, Wolanski and Hamner 1988).

Both Buldir's location and the feeding data presented here indicate that all foraging by Whiskered Auklets there takes place within the oceanic zooplanktonic community. There is a poorly-developed coastal community of zooplankton at Buldir, probably because of the narrow continental shelf around the island (Fig. 1). In addition, the two *Neocalanus* copepods, the hyperiid *P. pacifica,* and the pteropod *L. helicina,* are dominant members of this epipelagic oceanic

community (Fager and McGowan 1963; Cooney 1981, 1986, 1987).

Few other data on food habits of Whiskered Auklets are available for comparison with our results. Cottam and Knappen (1939) found that three of five birds from the Aleutians during summer contained copepods exclusively. The fourth stomach contained a mixture of amphipods, isopods, copepods, a scorpaenid fish, and a trace of a spider; the fifth stomach contained what appeared to be crustacean fragments and mollusc eggs. The only data on winter prey are from seven adults at the Commander Islands in December and January (Stejneger 1885). All but one of these birds were filled with gammarid and unidentified amphipods; the remaining one contained a small gastropod (a pteropod?) and the remains of a decapod.

Neocalanus copepods are seasonally-migrating species that are most abundant in surface layers from spring to early fall, whereupon they migrate to depths and reproduce in midwinter, using stored lipids for egg production (Heinrich 1962, Fulton 1973, Miller et al. 1984, Cooney 1987). Whiskered Auklets apparently become nearly-monophagous on *Neocalanus* copepods during summer, when the latter are abundant near the ocean's surface, but then probably switch to eating amphipods and other zooplanktonic crustaceans during winter, when the *Neocalanus* are living 600–1,000 m below the ocean's surface. At St. Lawrence Island, Least and Crested auklets took gammarid amphipods in number only when their "preferred" prey (copepods and euphausiids, respectively) were not common (Bédard 1969b). Further, when chicks of these two species were fed only gammarids, they consistently lost weight and died within 4 days. Hence, there may be a nutritional basis for the apparent preference for copepods.

The comparison of the food habits of the four species in late July/early August indicates that interspecific differences in prey eaten resulted from size-related differences in food preferences, rather than from differences in the availability of certain prey. That is, the two smaller auklets concentrated on *N. plumchrus* (about 5 mm in length), the smaller of the two large oceanic copepods, whereas the two larger auklets concentrated on the larger *N. cristatus* (about 10 mm in length) and *P. pacifica* about 10 mm in length). (Parakeet Auklets also took *E. isenbeckii* megalopae that were about 10 mm in length.) If (as we believe) turbulence from tidal mixing determines the vertical distribution of the main zooplankton species around Buldir, the four seabird species have to be selecting preferred prey on the basis of size out of a mixture of possible prey items.

Bédard (1969a) predicted that the small difference in size between Least and Whiskered auklets should cause extensive overlap in food habits, but comparative data on food habits from areas where the two species coexist were not available at that time. He further suggested that this (hypothesized) competition caused the paucity of Whiskered Auklets in the Aleutian Islands, where Least Auklets are abundant, and the abundance of Whiskered Auklets in the Kuril Islands, where Least Auklets are absent. Our small samples from the Aleutians indicate extensive overlap in prey between these two auklet species at Buldir, thus lending support to Bédard's hypothesis of interspecific competition. Interspecific competition for food may help shape the distribution and abundance of Whiskered Auklets, but additional studies of food habits and the prey base are required to test Bédard's hypothesis adequately.

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