JOHN F. PIATT AND ALEXANDER S. KITAYSKY

Fratercula corniculata

FRENCH: *Macareux cornu*
YUPIK ESKIMO: *Kupruwuk*
ALEUT: *Kageeach*
RUSSIAN: *Ipatka*
JAPANESE: *Tsunomedori*

Horned Puffin

HORNED PUFFIN

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Despite its ubiquitous appearance as a curio in gift shops, the Horned Puffin is a poorly studied member of the auk family. Distributed throughout subarctic waters of the North Pacific, its large breeding colonies are isolated and difficult to access. Unlike its close relatives, the Atlantic Puffin (*Fratercula arctica*), Tufted Puffin (*F. cirrhata*), and Rhinoceros Auklet (*Cerorhinca monocerata*)—which typically nest in burrows dug into soft soil—the Horned Puffin generally nests in rock crevices and on cliffs, making it difficult to access chicks or adults for routine studies of breeding biology.

Horned Puffins are known for carrying beakfuls of small fish to their young during the breeding season, and one might rightly conclude that they are well suited to living in coastal habitats that teem with abundant forage fish such as sand lance (*Ammodytes hexapterus*) and capelin (*Mallotus villosus*). However, this image belies their pelagic diet and ecology. While adults feed mostly fish to their chicks, they themselves consume a substantial proportion of squid and other invertebrates. During the non-breeding season, adults migrate far south to oceanic waters of the central North Pacific, where diets consist largely of bathypelagic lanternfishes and squid. Juveniles migrate south to the central North Pacific immediately after fledging and may not return to coastal breeding areas for

The Birds of North America
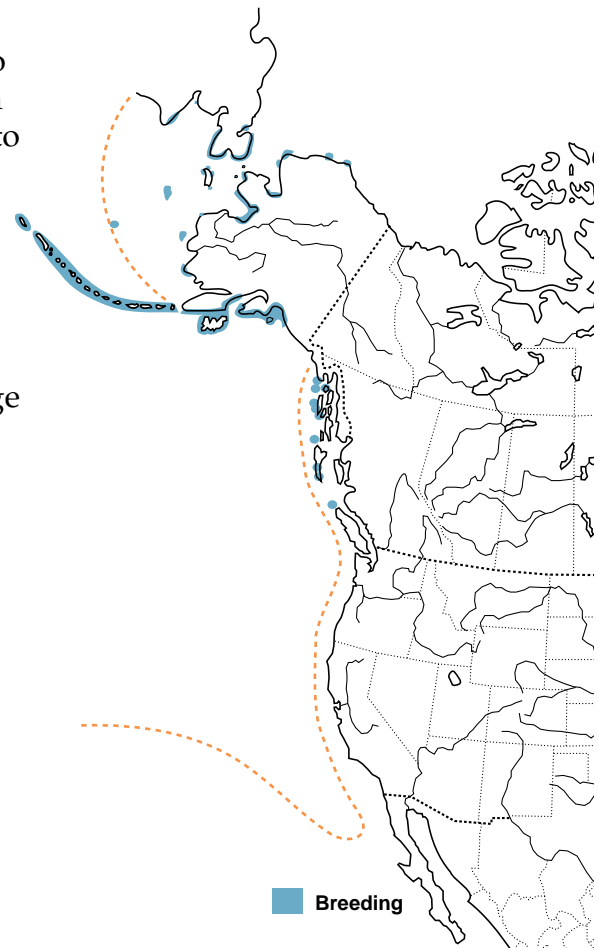Life Histories for the 21st Century

■ **Breeding**

Figure 1.
Distribution of the Horned Puffin in North America and easternmost Asia. This species winters north and south to the dashed line and breeds in other portions of Asia. See text for details.

several years. Thus, the Horned Puffin is truly a pelagic species, spending most of its life at great distances from land in the company of species we more typically consider oceanic, such as albatrosses and shearwaters.

Only a handful of studies have focused on Horned Puffins, although much incidental information is available from general seabird field investigations (Petersen 1983, Byrd et al. 1993). Sealy (1973) provided the earliest review of the biology of this species in the North Pacific, with details of breeding ecology on St. Lawrence Island. Soon after, Wehle (1976, 1980) and Amaral (1977) conducted graduate studies on Horned and Tufted puffins, adding a wealth of new information on breeding biology, behavior, chick growth, diets, and habitat use in the Gulf of Alaska and the Aleutians Islands. Since then, only a few studies have added substantially to our knowledge of Horned Puffins (Hatch and Hatch 1990a, 1990b; Kitaysky 1996; Harding 2001). For the future, studies of colony attendance behavior would be useful for establishing population monitoring protocols. More data on feeding ecology and breeding biology would be useful for assessing temporal and spatial variability in population biology.

DISTINGUISHING CHARACTERISTICS

Medium–large alcid (about 38 cm length) with large, laterally compressed, triangular bill. Breeding (Alternate)-plumage adults black with large white patch on face and white underparts from breast to under tail-coverts. Oversized bill is bright yellow with distal third red, variable number (2–6) of vertical grooves on distal third, and bright-orange rictal rosette at base of gape. Legs and feet bright yellowish orange to reddish. In flight, contrast between black chin and throat, white face, and white underparts creates appearance of a wide black necklace. At close range, a leathery dermal process, extending upward from eye (up to 12 mm) visible, creating horned appearance from which species' name derived. Male slightly larger than female, but sexes otherwise alike in appearance. Nonbreeding (Basic)-plumage adult similar to breeding adult, but white portion of face replaced by smoky grayish brown anteriorly and silver gray posteriorly and bill becomes smaller (rosettes and portion of outer bill covering at base of upper mandible absent) and duller (brown with distal portion reddish) but with grooves retained. "Horn" also absent, and legs and feet become pale fleshy color. Juvenile similar to Basic-plumaged adult, but bill shorter, narrower, entirely brownish gray in color and lacking grooves. Face-patch smoky black. Immature also similar to Basic-plumaged adult except (Basic I plumage) no grooves on bill, and (Alternate I plumage) less-developed nuptial bill ornaments.

Neck is short and retracted into shoulders in flight, giving stocky appearance. At sea, flight is rapid and direct, usually a minimum of 10–30 m above sea surface. Swims and dives well, takes off from water after gathering momentum. Walks upright with ease over rocks, clinging to surface with claws. Reclines with tarsus pressed flat, but walks on its toes.

Contrasting black-and-white plumage, combined with large triangular, laterally compressed bill distinguish this species from all other alcids within its range except Tufted Puffin. Horned Puffin distinguished from Tufted Puffin in all plumages by presence of white breast, while Tufted Puffin has dark breast or entirely dark underparts. Adult breeding Tufted Puffin also has mostly orange bill and distinctive, large, yellowish feather tufts along side of crown, lacking in Horned Puffin.

Horned Puffin closely resembles Atlantic Puffin, which occurs along Atlantic Coast of North America. Atlantic Puffin in breeding plumage lacks long process above eye, and base of bill is yellow and dark, not entirely yellow, as in Horned Puffin. In all plumages, white to gray patch on face extends down to chin and upper throat in Atlantic Puffin while face-patch extends down only to commisure in Horned Puffin. Face-patch of Horned Puffin contrasts with blackish chin and throat. In nonbreeding plumage, distal portion of Atlantic Puffin's bill also more yellowish than Horned Puffin. Distribution of Horned and Atlantic puffins entirely separate, and these species not expected to overlap geographically.

DISTRIBUTION

Widespread in North Pacific Ocean, from mid-Transition Zone (about 35°N) to Beaufort Sea. Nests on coastline and offshore islands in British Columbia (rare), Gulf of Alaska, Aleutians, Sea of Okhotsk, Kurils, Bering and Chukchi Seas. Winters over a broad area of the central North Pacific, generally over deep oceanic waters.

THE AMERICAS

Breeding range. Rare in British Columbia. Breeding documented on Anthony I. and suspected at several other locations (Campbell et al. 1990). About 76% of colonies and 87% of world population found in Alaska (Fig. 1). Largest colonies concentrated in nw. Gulf of Alaska along Alaska Peninsula in Semidi, Shumagin, and Sanak Is. Population dispersed among Aleutian Is. and a few islands in Bering and Chukchi Seas (e.g., Pribilofs, St. Matthew I., St. Lawrence I., Diomede Is.), and at a few coastal and island sites along Alaska mainland. Most northerly well-established colony is at Cape Lisburne in Chukchi Sea. Small numbers breed as far east as Cooper I. (east of Pt. Barrow) in Beaufort Sea (Divoky 1982).

SUMMER, NONBREEDING RANGE. Nonbreeders or prospectors observed regularly during spring and summer in coastal British Columbia, Washington, Oregon, and California (Hoffman et al. 1975, Roberson 1980) and about 200–800 km offshore (Pittman and Graybill 1985). Subadult and few adult birds are caught during summer in high-seas drift nets as far south as 35°N, suggesting year-round residence in central North Pacific (Intl. N. Pac. Fish. Comm. 1992; P. J. Gould unpubl.). Total bycatch in drift-net fisheries in Central Pacific, prosecuted mostly in summer, once may have exceeded 50,000 individuals/yr (DeGange et al. 1993), so summer populations there must be substantial. Pelagic surveys of region in summer also suggest similar populations (based on observed densities of 0.004–0.04 birds/km² in e. Subarctic and Transitional waters; Springer et al. 1999, JFP).

Winter range. Winters offshore, throughout North Pacific. Excluded from n. Bering and Chukchi Seas by ice in winter. Densities at sea in se. Bering Sea and Gulf of Alaska diminish greatly in fall and winter to <2% of summer densities (JFP and P. J. Gould unpubl.), suggesting most individuals move farther south (Gould et al. 1982). Rare on coastal Christmas Bird Counts in Alaska. Few remain as year-round residents in Aleutian passes (Gabrielson and Lincoln 1959). Casual along outer coast of British Columbia (Sealy and Nelson 1973, Campbell et al. 1990). Rarely seen along immediate Pacific Coast from Washington to California except during infrequent die-offs or "wrecks" (Roberson 1980, Pitman and Graybill 1985, Campbell et al. 1990). Far more common offshore in winter; e.g., >180 km off San Francisco, CA (Pitman and Graybill 1985).

OUTSIDE OF THE AMERICAS

Breeding range. About 24% of colonies and 13% of world population found in Russia. Nests as far north as Wrangel I. in Arctic Basin and northwest on Kolyuchin I. along n. Chukchi Peninsula, on e. and s. Chukchi Peninsula (Konyukhov et al. 1999), Big Diomede I., Ratmanova I., Anadyr Bay, Olyoumka I., along eastern part of Kamchatka Peninsula south to Kronotsky Bay, and Komandorskiye Is., northern part of Sea of Okhotsk, Talan I. (largest colony outside Americas estimated at 100,000 individuals), Shantar Is., Iona I., n. Primorie, Sakhalin I., and n. Kuril Is. (Kondratiev et al. 2000). Most southerly colony at Cape Terpeniye on Sakhalin I. Observations of birds around Hokkaido (n. Japan) in summer, some in association with Tufted Puffin colonies, but not known to breed in Japan (Brazil 1991).

Winter range. Excluded from Sea of Okhotsk and n. Bering Sea in winter by ice. Common in open waters around Kuril Is., s. Sakhalin I., Komandorskiye Is., s. Kuril Is.; occasionally winters around Hokkaido I. and ne. Honshu Is. (Kharitonov 1990). Wintering individuals recorded near Shantar Is. (Trukhin and Kosygin 1986). Rare in Japan during winter, with most southerly record near Tokyo (about 35°N) on outer coast (Brazil 1991).

Overwinters in a broad area of central North Pacific, ranging south to north from about middle of Transition Zone (about 35°N) to Subarctic waters off Alaska continental shelf and Aleutians; and west to east from Japan to California. Placed in Northern Transition guild of North Pacific seabirds, which regularly range from Subarctic to mid-Transitional waters (Gould and Piatt 1993). Central North Pacific likely an important nursery and overwintering area for juvenile and nonbreeding individuals (Gould et al. 1982). While densities at sea diminish in fall and winter on Gulf of Alaska shelf, densities in e. Subarctic Gyre increase at least four-fold in winter (Springer et al. 1999, JFP and P. J. Gould unpubl.). Bycatch records in high-seas drift nets place Horned Puffins well into Transitional waters (below about 40°N) during fall and winter (Int. N. Pac. Fish. Comm. 1992, P. J. Gould unpubl.). Horned Puffin carcasses have even been found in winter on beaches of the Hawaiian and Leeward Is. (about 20–30°N; Clapp 1986).

HISTORICAL CHANGES

No evidence of change in distribution. Anecdotal information from last 100 yr suggest neither expansion nor contraction of range. As for other seabirds, predation by introduced foxes (*Vulpes* spp.) may have eliminated or reduced populations on some islands, but details lacking for Horned Puffin (Bailey and Kaiser 1993).

FOSSIL HISTORY

In Pacific, only known puffin fossils are those of *Cerorhinca*, which Chandler (1991) synonymized into *Fratercula*. Holotype and only known specimen of *C. dubia* is an associated leg from late Miocene, Clarendonian (North American Land Mammal Age [NALMA] 9–10 Megannum [Ma]), of Lompoc, CA. The Dubious Puffin is slightly (2%) smaller than extant Rhinoceros Puffin [= Auklet] *C. monocerata* (*cf.* Chandler 1991). *C. minor* and *C. reai*, also from Pacific, are 25–30% smaller than Rhinoceros Puffin (Chandler 1991). *C. minor* is from late Miocene or early Pliocene, late Hemphillian (NALMA, 5 Ma) deposits on Cedros I., Baja California, Mexico. *C. reai* is from late Pliocene, late Blancan (NALMA, 2 Ma) from San Diego Co., CA. In Atlantic, earliest puffins known (Olson 1985) from late Miocene to early Pliocene (about 5 Ma), including *Fratercula* and possibly *Lunda* (now synonymized with *Fratercula*).

SYSTEMATICS

GEOGRAPHIC VARIATION; SUBSPECIES

Monotypic and no subspecies have been described or proposed (Gibson and Kessel 1997, Gaston and

Jones 1998). Geographic variation poorly described. Measurements of body mass and wing length suggest cline of increasing size from south to north (see details in Measurements, below).

RELATED SPECIES

Phylogenetic analyses of Alcidae based on morphological and ecological characters (Strauch 1985), as well as allozymes and direct sequencing of mitochondrial DNA (mtDNA; Moum et al. 1994, Friesen et al. 1996), agree that Alcidae comprises 6 distinct lineages. Analysis of total molecular evidence (mtDNA and allozymes) indicates that Fraterculini includes Rhinoceros Auklet, in basal position, and puffins (*Fratercula*), with Atlantic and Horned puffins as sister species (Friesen et al. 1996, Am. Ornithol. Union 1998). Fraterculini probably sister to auklets (Aethini), but relationships among the 6 groups of alcids difficult to resolve due to apparently rapid and ancient basal radiation. Divergence of alcids and divergence of puffins from true auklets likely occurred in late Miocene (10–12 Ma). Radiation of puffins in Pacific came much later, during second major Pliocene glaciation (2.3–2.5 Ma) when puffins diverged into a subarctic/boreal form (Rhinoceros Auklet) with brown plumage and nocturnal behavior, and an arctic/subarctic form with specialized claw for digging burrows (leading to other puffins). This split was followed about 0.3 Ma later by divergence of an all-black lineage (leading to Tufted Puffin) and a lineage with eye scales (leading to Horned and Atlantic puffins). Atlantic and Horned puffins apparently diverged when Bering Strait was open at beginning of Nebraskan glaciation (about 1.5 Ma). Confounding this story (by V. L. Friesen, JFP, and A. J. Baker unpubl.) are presence of puffin fossils in Atlantic from early Pliocene (see Distribution: fossil history, above). It is possible that *Fratercula* entered Atlantic in late Miocene (Olson 1985) and that the Horned Puffin represents a recent return migration of the Atlantic Puffin stock into the Pacific (Gaston and Jones 1998).

MIGRATION

NATURE OF MIGRATION IN THE SPECIES

As in other alcids, migration not complete. In Bering Sea and Sea of Okhotsk, Horned Puffins are necessarily pushed south by advancing ice in winter. Some remain near breeding colonies in Aleutians and Gulf of Alaska, but most undergo general postbreeding dispersal to overwintering grounds in central North Pacific (see Distribution, above) where juveniles possibly remain for 1–2 yr before returning to breeding areas (Gould and Piatt 1993). Adults return to colonies en masse in spring (Wehle 1980).

TIMING AND ROUTES OF MIGRATION

Pelagic areas of Bering Sea and Gulf of Alaska mostly (>95%) vacated by Nov. No specific migratory routes; postbreeding dispersal and movement over a large area of North Pacific. Return to colonies consistent from year to year; at Semidi Is. arrived 14–20 May in 5 yr of study (Hatch and Hatch 1990a). Arrival earlier at lower latitudes (Wehle 1980): early to mid-May at Buldir I. (52°N), mid- to late May at Shumagin Is. (55°N) and Semidi Is. (56°N), late May at St. Lawrence I. (63°N), and early Jun at Little Diomede I. (65°N) and Cape Thompson (68°N). Correspondingly, departure dates earlier in southern colonies (early Sep) than northern ones (late Sep).

MIGRATORY BEHAVIOR

Nothing known about migration behavior at sea. First arrival of birds at colonies generally consists of a few individuals appearing offshore, followed within days by population arriving en masse (Wehle 1980). Attendance is highly variable, with birds settling and departing from nesting areas over 3- to 6-d periods until egg-laying, when fluctuations diminish in amplitude (A. Harding and JFP unpubl.). Laying, hatching, and fledging are fairly synchronous, so departure from colonies occurs over a 2- to 3-wk period as chicks fledge. Individuals probably leave colonies for wintering areas immediately after chicks fledge.

CONTROL AND PHYSIOLOGY

No information.

HABITAT

BREEDING RANGE

Breeds colonially on barren islands and mainland cliffs. Where mammalian predators (e.g., foxes) are present, breeding usually restricted to inaccessible cliff crevices; where predators absent, uses talus slopes, cliff crevices, and boulders along beaches (see Breeding: nest site, below). Breeds on small (<1 ha) islets and rocks, but largest colonies on substantial offshore islands (>1–10 km²) scattered widely around the coast of mainland Alaska and far offshore in the Aleutians and Bering Sea. Climate throughout breeding range generally cool (<15°C), wet (persistent rain and fog), and overcast during summer.

Forages in low densities (0.1–2.0 individuals/km²) in bay, shelf, and shelf-edge habitats throughout Alaska (Hunt et al. 1981b; Gould et al. 1982; Piatt et al. 1990c, 1992; Elphick and Hunt 1993; Piatt 1993); generally with 100 km of colonies (see Food habits, below). Tends to forage more offshore than coastally. Offshore distribution in Gulf of Alaska further indicated from carbon stable isotope analyses of muscle tissue, suggesting that Horned Puffins distributed more offshore than Common Murres (*Uria aalge*),

Cassin's Auklets (*Ptychoramphus aleuticus*), and other shelf-foraging alcids, and exceeded only by storm-petrels (*Oceanodroma* spp.) in use of offshore feeding habitat (Hobsen et al. 1994).

WINTER RANGE

Few individuals found in coastal or shelf areas during winter. Whereas some may overwinter in passes among Aleutian Is. (Gabrielson and Lincoln 1959), majority appear to inhabit deep, oceanic waters of central North Pacific (see Distribution, above). This vast area consists of Subarctic, Transitional, and Subtropical Domains characterized by fairly uniform water properties from west to east (Japan to California), but with large property gradients from north to south (Alaska to Hawai'i; Gould and Piatt 1993). Oceanic habitat is influenced by physical processes such as currents and water mass boundaries, vertical stratification, and surface mixing from storms. Abundant forage species in Central Pacific include squid, lanternfish (Myctophidae), northern smoothtongue (*Leuroglossus stilbius*), Pacific saury (*Cololabis saira*), and euphausiids (Springer et al. 1999).

SPRING AND FALL MIGRATION

No information.

FOOD HABITS

FEEDING

Main foods taken. Morphology of tongue and bill are intermediate between fish- and plankton-eating alcids (Bedard 1969). Correspondingly, about 20–30% of adult diet is invertebrates and the remainder fish, but adults feed almost exclusively fish to young (Wehle 1982, 1983). During breeding season, mostly small schooling fishes such as sand lance, capelin, juvenile pollock, greenling, salmonids; adults also take squid, octopus, polychaetes, and euphausiids. In nonbreeding season, predominantly myctophids and squid (P. J. Gould unpubl.).

Microhabitat for foraging. In Chukchi Sea (Piatt et al. 1990c), n. Bering Sea (Piatt et al. 1992, Elphick and Hunt 1993), s. Bering Sea (Hunt et al. 1981b), and Gulf of Alaska (Piatt 1993), forages widely in stratified waters within 100 km of colonies. Previous investigators suggested that Horned Puffins foraged mostly within 1–2 km of colonies (e.g., St. Lawrence I. [Sealy 1973], Big Koniuji [Moe and Day 1977], Buldir [Wehle 1980]). While some individuals do forage near colonies (JFP) where islands themselves promote local productivity, most forage at much greater distances. Wehle (1976) frequently observed Horned Puffins at distances of 10–60 km on transects from Buldir I. Similarly, Diomede Is. are locally productive and many Horned Puffins forage nearby, but they are also widely distributed in stratified Bering Shelf and Alaska

Coastal Current waters up to 50 km from colony (Piatt et al. 1992). Horned Puffins at Cape Thompson in Chukchi Sea forage mostly in Alaska Coastal Current waters within 30 km of colony, but were observed on transects 120 km from Cape Thompson (Piatt et al. 1990c). At Chisik I. in lower Cook Inlet, Horned Puffins eat mostly sand lance, which are relatively scarce around Chisik (Robards et al. 1999b), and surveys reveal most Horned Puffins routinely forage 50–110 km away (JFP). In short, Horned Puffins forage over a wide area of continental shelf and shelf edge in Gulf of Alaska and Bering Sea during breeding season; little support for earlier conclusions that foraging is restricted to only a few kilometers from colonies.

Association with fine-scale oceanographic features not well described, perhaps owing to generally low densities in most areas. In Bering and Chukchi Seas, clear preference for well-stratified Alaska Coastal Waters (Piatt et al. 1990c, Haney 1991, Elphick and Hunt 1993). Large feeding flocks observed near island headlands or straits where rip currents concentrate prey (Wehle 1976, Hoffman et al. 1981, Hunt et al. 1988). In contrast to some other alcids, not particularly attracted to fronts between water masses, convergent slicks, or well-mixed waters (Haney 1991, JFP). Frequent use of shallow, nearshore areas may be linked to preferential use of this habitat by sand lance (Robards and Piatt 1999, Robards et al. 1999c).

Food capture and consumption. Prey captured underwater using wing-propelled flight at speeds of 1–2 m/s (Piatt and Nettleship 1985). Dive depths unknown, but a function of body size in Alcidae; maximum depths estimated from regression as 77 m (for 532-g bird; Burger 1991). Usual dives shallower; most probably <30 m. Captive Horned Puffins seldom foraged near bottom, in contrast to Tufted Puffins and Pigeon Guillemots (*Cepphus columba*), and more commonly searched horizontally while underwater (Duffy et al. 1987). Birds capture and eat prey underwater, except food they carry to chicks. Adapted for capturing and carrying many fish in bill at one time (Bedard 1969) and routinely carry 5–20 fish in deliveries to chicks (bill-loads), with observed maximum of 65 larval fish (Wehle 1983, JFP). Feeds during day and at dusk; possibly also at night based on common presence of lanternfish in diet during winter.

Usually forages in small groups, sometimes in association with other fish-feeding seabirds such as Black-legged Kittiwakes (*Rissa tridactyla*), Glaucous-winged Gulls (*Larus glaucescens*), murres (*Uria* spp.), auklets (*Aethia* spp.), and Tufted Puffins (Hoffman et al. 1981, Hunt et al. 1988). May respond to flock catalysts or initiate feeding on fish schools themselves. Independent of mixed-species flocks, foraging group size is typically small. Median size of flocks on water is just 2 individuals ($n = 656$ flocks examined in Bering Sea and Gulf of Alaska; JFP). Flocks of 5–20 birds may form in association with large prey schools and mixed-

flock feeding assemblages (Hoffman et al. 1981), and in rare circumstances feeding aggregations of hundreds or thousands may form near large colonies where strong currents create tide rips and concentrate prey (e.g., Semidi Is. [Hoffman et al. 1981], Shumagin Is. [JFP]). Usual pelagic densities are 1 or 2 birds/km^2.

DIET

Relatively good information for nestlings, limited for adults.

Nestlings. Almost entirely fish. Remarkable dependence (averaging 65% of diet) on sand lance throughout an enormous range of North Pacific (Appendix 1), from Cook Inlet (Chisik and Barren Is.), along Alaska Peninsula (Suklik, Shumagin, Midun, High, Sozavarika Is.), to w. Aleutians (Buldir I.) and Sea of Okhotsk (Talan I.). Prior to large-scale change in forage-fish communities in Gulf of Alaska during late 1970s (Anderson and Piatt 1999), capelin was important component (20–50%) of chick diets at some colonies (Barren, Shumagin Is.). Capelin practically disappeared from diets of many seabirds in 1980s (Piatt and Anderson 1996), being replaced largely by gadids such as juvenile walleye pollock (*Theragra chalcogramma*) and Pacific cod (*Gadus macrocephalus*). Gadids now make up a significant portion of diets (up to 30%) at some colonies (Appendix 1). Besides common prey, Horned Puffins feed chicks few other species, especially in comparison to Tufted Puffins (Hatch and Sanger 1992). For example, of 45,743 prey collected from both species in 1988–1994 (JFP, J. Williams, and G. V. Byrd unpubl.), Tufted Puffin chick diets included 47 different species, whereas Horned Puffin included only 20 species, with only 7 taxa making up >1% of diets each. Hatch and Sanger (1992) reported similar results. Less important taxa may be common at some sites in some years. Rock and kelp greenling (*Hexagrammus* spp.) were common at Suklik I. in 1985–1987 (2.3%) and in 1991–1994 (7.1%) and Buldir I. in 1988–1991 (14.6%). At Buldir I., an oceanic island where sand lance and capelin habitat is scarce (Springer et al. 1996), Atka mackerel (*Pleurogrammus monopterygius*) was common (42%) in 1975 (Wehle 1983). Juvenile salmonids were common at Chisik I. (4.5%) in 1998 and at Talan I. (13%) in 1987. Herring (*Clupea harengus*) were common at Talan I. (54%) in 1987. Overall, invertebrates make up a small part of chick diets (Appendix 1). Principal taxa are squid (Gonatidae) and euphausiids (mostly *Thysanoessa* spp.).

Fish delivered to chicks normally range in size from about 30 to 160 mm, and average about 70 mm (Wehle 1983, Hatch and Sanger 1992). These sizes correspond to age 0 pollock; ages 0–2 sand lance; and ages 1–3 capelin (Hatch and Sanger 1992). Bill-loads may include only 1 or 2 larger fish or dozens of small, larval fish. Numbers of fish delivered/load can, therefore, vary widely (range 1–65), but average 6.8 fish/load (n = 13 colony-years; Wehle 1983; Hatch and Sanger 1992;

Harding 2001; JFP, J. Williams, and G. V. Byrd unpubl.). On average, adults delivered 9.3 g/load (n = 12 colony-years). However, meal sizes probably underestimated in most studies because adults will partially eat meals bound for chicks if investigators prevent delivery of food (Piatt et al. 1997).

Adults. Few data, scattered widely in time and space. In Chukchi Sea (Cape Thompson), diet includes gadids (Arctic cod; *Boreogadus saida*), sand lance, capelin, and invertebrates (Appendix 2). In Bering Sea (1975–1984), gadids (juvenile pollock) common, followed in order of importance by greenling, sand lance, and sand fish (*Trichodon trichodon*; Hunt et al. 1981a). Invertebrates, mostly squid and some polychaetes, copepods, decapods, amphipods, and euphausiids, made up a significant portion (38–48%) of diets by number or weight. In w. Aleutians (Buldir I.) during 1975, invertebrates (squid and polychaetes) dominated (fish were unidentified; Wehle 1982). Birds from Aiktak, Unalaska, Chagulak, Buldir, and Agattu Is. preyed on pollock and sand lance, while squid and polychaetes made up about a third of diets (Springer et al. 1996, JFP). In Gulf of Alaska (mainly Chisik, Barren, Kodiak, Semidi, Mitrofania, and Shumagin Is.), capelin and sand lance dominated diets prior (1969–1978) to regime shift in late 1970s (Piatt and Anderson 1996); in more recent years (1988–1998), capelin in diet largely replaced by gadids, principally pollock (44.5%) and Pacific cod (5.5%). Other fish included myctophids, flatfish, and sculpins (Cottidae).

Invertebrates (mostly squid, euphausiids, polychaetes, and amphipods) made up 13–20% of diets. Whereas traditional diet studies indicated that adults feed at a trophic level of 4.0, nitrogen isotope analysis suggested a trophic level of 3.4—indicating a diet with significant proportion of euphausiids and other invertebrates (Hobsen et al. 1994).

Only 4 adult sampling efforts (Appendix 2) coincident in time and space with chick meal sampling (Appendix 1) permit contrast between adult and chick diet. Adults at Buldir I. (Wehle 1982) consumed mainly squid in 1975 (Wehle 1982) and 1988 (Springer et al. 1996), while feeding mostly sand lance, greenling, or Atka mackerel to chicks (Wehle 1983, J. Williams and G. V. Byrd unpubl.). Adults in Gulf of Alaska during 1969–1978 (Sanger 1983) ate mostly capelin and sand lance, and fed same to chicks (Manuwal and Boersma 1977, Moe and Day 1977, Amaral 1979), but took 13% invertebrates as well. In more recent years (1988–1998) adults ate 20% invertebrates (mostly squid), while feeding chicks mostly sand lance and gadids (Hatch and Sanger 1992; JFP, T. van Pelt, and S. A. Hatch unpubl.). Thus it appears that adults try to maintain chicks on nutritious fatty fishes (van Pelt et al. 1997), while consuming less valuable prey themselves. Adults consume more fish in shelf habitats and less fish at colonies where shelf habitat is scarce (Springer et al. 1996).

Subadults, adults in winter. Diets of subadults or adults away from breeding colonies are known only from birds collected during studies of bycatch in central North Pacific drift-net fisheries (P. J. Gould unpubl.). Fisheries observers recorded 148 Horned Puffins entangled in drift nets during 1989–1991 fishing seasons, with most bycatch occurring between 170°E–170°W and 36–42°N. Most records were of single birds collected May–Nov. Of 18 birds recovered and examined for stomach contents, 16 were subadults with large bursa (collected Jun–Jul) and 2 were adults (collected May and Nov); 8 contained only fish, 11 contained only invertebrates, 1 contained both fish and invertebrates, and 1 contained only cephalopods. Fish dominated diets by weight (52%). Of 118 prey items identified (Appendix 2), most ($n = 93$) were fish and most ($n = 83$) of these were myctophids (lanternfish), including 8 species; principally *Ceratoscopelus warmingii* ($n = 24$), *Electrona risso* ($n = 17$), and *Lampanyctus jordani* ($n = 7$). Cephalopods were also common ($n = 25$) and included the squids *Ommastrephes bartrami* ($n = 16$) and *Onychoteuthis borealijaponica* ($n = 6$).

These data suggest that Horned Puffins, like many other marine birds and mammals in the North Pacific (Springer et al. 1999), depend on oceanic myctophids and squid when away from breeding areas. Atlantic Puffins collected during winter away from breeding colonies revealed a similar reliance on myctophids (37% *Benthosema glaciale*), squid (43%), and polychaetes (13%; Falk et al. 1992). In coastal areas in winter, Atlantic Puffins relied mostly on euphausiids (82%), other invertebrates (9%), and fish (8%).

FOOD SELECTION AND STORAGE

Does not store food. Narrow diet suggests selection of preferred prey, especially those with high nutritive and caloric value for chicks. Only one study of food taken versus availability (Harding 2001, JFP). At Chisik I. in 1995–1996, adults fed chicks 94% sand lance (Appendix 1) and ate 95% sand lance themselves ($n = 13$ stomachs, 177 prey items). Midwater trawls ($n = 6$) around Chisik in 1996 caught 19 species of fish, with capelin (25.5%), pollock (22.2%), and sand lance (23.9%) being about equal in abundance (Robards et al. 1999b). Similarly, nearshore seine sets ($n = 30$) in 1996 caught 24 species, of which sand lance ranked second in catch-per-unit effort, and fifth in frequency of occurrence (Robards et al. 1999b). Thus, proportions consumed in diets were greater than available locally, suggesting selection for sand lance.

NUTRITION AND ENERGETICS

No direct measures of energetic or nutritive requirements of adults. Energy demand of chicks increases with age. Average daily energy requirement for captive chicks fed *ad libitum* was 528.9 kJ/d (fledging at 45 d; Kitaysky 1996). For wild chicks with minimal feeding rates and long development time (55 d), average daily intake 259.5 kJ/d. Other measures of daily needs for wild chicks: 475.5 kJ/d (Talan I.) and 308.34 kJ/d (Semidi Is.).

Nutritive value of food largely a function of fat and protein densities. Protein content varies little among fish. Amino acid composition of proteins may vary considerably and affect growth but little is known about amino acid requirements in seabirds (Montevecchi and Piatt 1984). Energy density (kJ/g wet mass) of common prey eaten by Horned Puffins in Alaska during summer varies widely among species (mean sizes 50–165 mm): Atka mackerel, 4.02; capelin, 4.45; greenling, 3.45; myctophid, 8.05; cod, 2.94; pollock, 2.73; sand lance, 4.60; squid, 3.81 kJ/g wet mass (van Pelt et al. 1997). Energy densities also vary widely among seasons for different taxa, and seasonal patterns depend on life history. Mature sand lance spawn in Oct; achieve peak energy densities in Jul (5.67 kJ/g wet); minimal energy densities in winter (Feb; 3.24 kJ/g wet; Robards et al. 1999a). In contrast, capelin spawn in Jun; achieve minimal energy densities in Jun–Jul (3.9 kJ/g wet), and peak in Dec (9.4 kJ/g wet; Montevecchi and Piatt 1984).

METABOLISM AND TEMPERATURE REGULATION

No measurements of field metabolic rate. Resting metabolic rate (RMR) of captive-reared chicks (Kitaysky 1996) can be estimated from regression equation: $\log RMR(kJ/d) = 0.867 + 0.70 \log MASS(g)$. Puffin chicks adjust metabolic rate to food supply, and can reduce metabolic rate by at least 47% during food shortage. Captive subadult consumed 40% of body mass on average, but daily food intake varied between 20 and 50% in cycles of 3–6 d, suggesting hunger and feeding behavior are regulated by endocrine system (JFP). No information on temperature regulation.

DRINKING, PELLET-CASTING, AND DEFECATION

No information on drinking; metabolic water obtained from food. Does not regurgitate pellets. Adults defecate outside nest chamber in burrow or in side chamber from main chamber (JFP and ASK). Chicks defecate at nest site when small; defecate at burrow entrance when older.

SOUNDS

VOCALIZATIONS

Development. Chicks make continuous *peep, peep, peep . . .* sound (Fig. 2), especially when hungry, or when adult returns with food. Adult-type vocalizations develop in first winter (captive chicks; JFP).

Vocal array. Little studied. Vocal at colonies, also in social gatherings at sea. Repertoire consists of call notes given by both sexes (see Fig. 2). Calls are similar to Atlantic Puffin's: a low growling "*arrr*" either

single or uttered 3 times in slow succession, the first being the highest one and each of the following lower than preceding (Lockley 1934). When threatened or fighting, utters similar growl but more sharply (Amaral 1977). On occasions when caught or harassed, birds utter a lower growl (Amaral 1977). During Head-Jerking behavior (see Behavior: sexual behavior, below), utter a soft sound "*op*," which sometimes forms a prolonged rhythmic "*op-op-op-op*." (Kharitonov 1990).

Wehle (1980) described 4 different types of calls with different functions:

SHORT "ERRR." Primary function is threat or warning.

PURRING. Similar to Short "*Err*" growl but longer in duration and softer, having the low purring quality of a cat. Function unknown; heard from birds resting at colony.

BISYLLABIC CALL. Growl characterized by a short, sharp "*er*" syllable followed by a higher pitch and longer syllable. Heard at colony and on water.

MULTINOTE CALL. Growl consists of 6 or 7 syllables (Fig. 2). First 2 syllables similar to Bisyllabic Call (above); third syllable higher in pitch than the first 2, the remaining 3 or 4 syllables match the initial "*er*"; i.e., "*er errr er er er er er*." Usually made by birds in burrows during pre-egg and early incubation, suggesting possible sexual function. Also during chick-rearing when visiting burrow.

Phenology. No quantitative information. No information outside breeding season, although captive subadults vocalize year-round (JFP). Calls heard throughout period of colony attendance, with greatest activity during egg-laying and incubation.

Daily pattern. Most vocalization takes place during daytime activity period, both at colony and on water. Like Atlantic Puffin, mostly silent at night.

Places of vocalizing. Highly vocal at colony, while standing on talus or grassy slopes outside nest-site, in social resting areas, and especially inside nesting crevices or burrows. Some vocalization on water where gathered in social aggregations, especially during interactions with other birds.

Social context and presumed functions. See above.

NONVOCAL SOUNDS
No information.

BEHAVIOR

LOCOMOTION
Walking, hopping, climbing. Walks upright with ease over rocks, clinging to surface with claws. Capable of hopping. Adept at climbing scree and cliffs. Reclines with tarsus pressed flat, but walks on toes.

Flight. Direct and powerful, but not very maneuverable (midair collisions among individuals circling above breeding colonies not uncommon). Uses
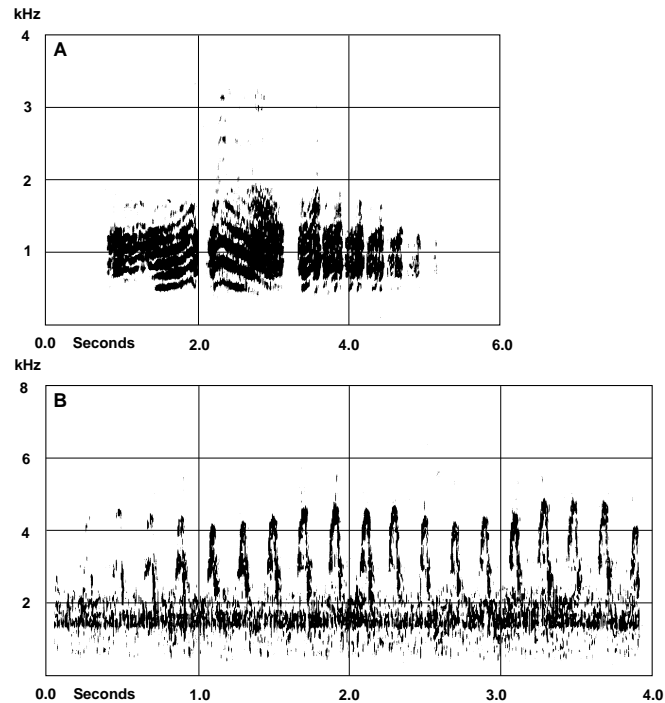

Figure 2. A. Multinote call of an adult Horned Puffin. B. Peep-peep call of chick. Recorded at Duck I., AK, Jul 1998, by Thomas van Pelt (U.S. Geol. Surv.). Prepared by staff of Borror Laboratory of Bioacoustics, The Ohio State University, using a Kay Elemetrics DSP 5500 Sona-Graph (with effective frequency resolution of 75 and 150 Hz for the adult and chick, respectively, and a 200-point FFT transform size for both).

feet as rudders. Takes off from water after gathering momentum, sometimes using feet as paddles until airborne. On land, takes off from angled slopes and elevated rocks or walks to cliff edge before initiating flight. Travels in small groups of 2–15 individuals on commute between nesting and foraging grounds; usually flies at altitude of 10–30 m above sea surface. Occasionally forms mixed flying flocks with Tufted Puffins or murres, but cannot keep up with them for long (I. L. Jones pers. comm., JPF, ASK).

Swimming and diving. Swims on surface by paddling with feet. Powerful underwater swimmer and diver. Similar to other alcids, propels itself under water by using flightlike beating of half-opened wings. Estimated maximal diving depth, using equation between body mass and maximal diving depth for Alcidae (Burger 1991), 77 m (see Food habits: feeding, above).

SELF-MAINTENANCE
Preening, stretching, bathing. Three types of body-maintenance behaviors described (Wehle 1980):

HEAD-DIPPING. During swimming, Head-Dips by submerging head above eyes into water. May be repeated frequently with head-shaking to eliminate water.

WING-FLAPPING. Erects itself on water, fluffs feathers, and vigorously flaps wings 7–10 times. Also flaps wings when it lies on one side so that one wing is under water while other is vertical to water; after bathing on one side, turns on other and repeats Wing-Flapping (ASK).

PREENING. Preens on land and water. Side of bill repeatedly rubbed on uropygial gland and secretion smeared over body feathers while preening and arranging feathers (ASK).

Sleeping, roosting. During daylight, breeding individuals sleep and roost in nest, in roosting areas at breeding colony, and on water close to colony. At night, spends time in nest or on water in vicinity of breeding colony (JFP, ASK).

Daily time budget. No information.

COLONY ATTENDANCE BEHAVIOR

Daily pattern of attendance at the colony. Attendance erratic early in season. During mating and pre-egg–laying, individuals spend morning hours in rafts close to colony (Amaral 1977). In late morning, disperse in colony, spending time on pair-bond maintenance, nest-site selection and defense, and burrow/crevice excavation and maintenance. During egg-laying, incubation, and early chick-rearing, diurnal attendance is typically bimodal, with peaks in morning and especially evening hours, with period of near-absence during midday (13:00–15:00; Wehle 1976, Harding 2001). Numbers usually build up on water first, then on breeding slopes or talus as birds move from water to land. By mid- to late chick-rearing, attends throughout day, but peak numbers still observed in evening (Harding 2001). Considerable variation in diurnal attendance patterns from day to day.

Attendance in relation to time of year. Present at colonies only during breeding season: May–Sep in Alaska (see Migration, above). Daily attendance during breeding season varies widely with peaks at intervals of 3–6 d (Petersen 1983); or 2–10 d on Buldir I. (I. L. Jones pers. comm.). Cause of fluctuations unknown, perhaps related to food supply and/or metabolic control of foraging behavior (see Food habits: metabolism and temperature regulation, above). At Chisik I., attendance most erratic at start of breeding season, more stable and generally highest during incubation, lower and more erratic as nestling period progresses (Harding 2001). No information on proportion of local breeding population present during activity peaks, nor whether individuals present in one peak are same birds observed in following peak.

AGONISTIC BEHAVIOR

Physical interactions. Fighting common in social gatherings and on slopes near nest sites, usually result of one bird trespassing on another's territory (Wehle 1980). May chase and threaten intruder with up-raised wings or Bill-Gaping. If threat display ignored, fighting may ensue; birds usually lock bills or grab napes and beat each other with wings, often tumbling down slope or cliff, still locked together. A deep guttural sound may accompany fighting. A pair might respond to presence of conspecifics by Billing with each other until intruder leaves (Wehle 1980).

Communicative interactions. In aggressive display, individual silent, threatens intruder by holding bill open for several seconds, shaking head, and approaching. Intraspecific aggressive behavior similar to that of Atlantic Puffin and other alcids. Several forms of aggressive posture (Wehle 1980, Kharitonov 1990):

FORWARD THREAT POSTURE. Bill kept closed, body and head horizontally directed toward a subject of aggression.

HEAD-FLICKING. Head jerked upward and bent toward back, bill directed up, wings often lifted and half-spread. May hold position for tens of seconds.

BILL-GAPING. Individual stands erect with neck stretched upward and bill facing recipient of threat. Neck- and head-feathers ruffled. Mandibles held wide apart, exposing brightly colored mouth-lining; tongue may protrude. May occur in response to intrusion on territory; before, during, or after a fight; and when a third bird attempts to join in Billing ceremony of a pair.

Other forms of communication include (Wehle 1980, Kharitonov 1990):

DEMONSTRATIVE GAIT. During this territorial display, body rocks from side to side, and steps are small and abrupt. Individual appears to walk in same place, and each step appears forced.

LANDING DISPLAY. Displays immediately after landing. Body held low to ground with wings outstretched above back. Head may also be outstretched in line with body or bent downward to varying degrees. Position held for several seconds. At conclusion of display, bird takes several exaggerated steps in this posture before slowly closing wings and resuming normal posture.

SPACING

Territoriality. Territorial behavior not well known (Kharitonov 1990). Pairs defend nest entrances. Males defend females at colony and on water. Mates of same pair perform joint flights near colony (Wehle 1980). Density of nests varies among colonies and nesting habitats. Minimal distance (mean ± SE) between nearest neighbor nest entrances varies between 0.91 m ± 0.08 on boulder slopes (n = 18) and 3.3 m ± 0.48 at cliff faces (n = 10; Petersen 1983; see also Breeding: nest site, below).

Individual distance. No information.

SEXUAL BEHAVIOR

Mating system and sex ratio. Socially monogamous as in Atlantic Puffins (Harris 1984), no quantitative

information on extra-pair fertilizations. Sealy (1973) suggested 1:1 sex ratio, and this is supported by other collections (Appendix 4).

Courtship and mate choice. Courtship mostly on water, less so on colony (Amaral 1977); begins with 2 individuals swimming side by side, then male lifts head with bill straight up while opening and closing bill in slow motion and jerking head. Male periodically bends neck and places head on back. Female assumes a hunched, low-to-water posture with head and neck held close to body. Male demonstration is followed by Billing, when male and female face each other and repeatedly rub bills together. Occasionally, both partners Head-Jerk at each other. Then male approaches female from behind, mounts female, keeping a balance by frequent beating of lifted wings. Copulation lasts on average 35 s (range 25–40 s; Amaral 1977). After mating, female usually dives and surfaces a few meters from male and then both partners flap wings. Two behaviors frequently observed in courting:

BILLING. Important component of sexual and social behaviors (Wehle 1980). Adults in pair stand facing, with bills side by side, and waggle heads while opening and closing bills. Although Billing occurs during courtship, it continues through reproductive season and may be observed between neighbors and individuals of same sex. During Billing, male sometimes grabs feathers on female's neck (Kharitonov 1990). Between Billings, partners occasionally bow toward each other and sometimes male ends Billing by grabbing female's leg above tarsus (Kharitonov 1990).

HEAD-JERKING. As in Tufted Puffin, uses Head-Jerking in courtship. In contrast to Tufted Puffin, may use Head-Jerk, in less exaggerated form, in other contexts as well (Wehle 1980). Head-Jerking observed in groups of birds on water, when not directed to a particular bird; spectators of a courting pair sometimes follow them and Head-Jerk. During Head-Jerking, individual utters a sort of *op* sound during prolonged Head-Jerking utters a rhythmic *op-op-op-op* (Kharitonov 1990).

Pair bond. Unknown whether pairs breed together in successive years, but likely since found in Atlantic Puffin and Rhinoceros Auklet (Harris 1984, Gaston and Dechesne 1996). Pair-bond behavior includes display with nest material and Billing. During nest defense, residents always retain nest site, suggesting advantage of early arrival and settlement at colony by breeding pairs (Amaral 1977).

Extra-pair copulations. No information.

SOCIAL AND INTERSPECIFIC BEHAVIOR

Degree of sociality. Colonial breeder. Nests in colonies of tens to thousands, sometimes larger (see Demography and populations: population status, below). Highly synchronized phenology (Amaral 1977) and reproduction in large colonies suggest a high degree of sociality. Forages in flocks of 2–10 individuals, sometimes gathering in much larger aggregations (see Food habits: feeding, above). Social behavior includes fly-bys (Wehle 1980); common during pre-egg stage and continuing throughout breeding. Birds make repeated circular flights above breeding colony before landing at colony or surfacing on nearshore waters in rafts. May consist of a few individuals or almost entire breeding population; function unclear. Also observed in other puffins and auklets.

Play. No information.

Nonpredatory interspecific interactions. Forms multispecies feeding flocks with other alcids and gulls (Hoffman et al. 1981). At multispecies colonies, may compete with Tufted Puffins for nesting habitat (Sealy 1973). Typically nests in rock crevices; Tufted Puffins generally use burrows in grassy slopes. On 2 occasions at Talan I., Horned Puffins lost rock-crevice nests to Tufted Puffins, which destroyed nests and eggs of former owners (ASK). Horned Puffins may out-compete Tufted Puffins in rock-crevice nesting habitats because more crevices are accessible to their smaller bodies. Might compete for nest sites with guillemot species (Divoky 1982). At Talan I., Horned Puffins attempted (but failed) to secure nests occupied by Spectacled Guillemots (*Cepphus carbo*; V. Zubakin and S. Kharitonov pers. comm.; ASK). Circumstantial evidence suggests Horned Puffins destroy Least (*Aethia pusilla*) and Crested (*A. cristatella*) auklet eggs, chicks, and adults where species share breeding habitat on Buldir I. (I. L. Jones pers. comm.).

PREDATION

Bald Eagles (*Haliaeetus leucocephalus*), Peregrine Falcons (*Falco peregrinus*), red fox (*Vulpes vulpes*), and river otter (*Lutra canadensis*) take adults during breeding season where they co-occur (Amaral 1977, Moe 1977, Bailey and Kaiser 1993). At Big Koniuji I., diet of Bald Eagles up to 13% Horned Puffins, diet of red fox up to 50% Horned Puffins, and combined predation by eagles, fox, and falcons made up about 2% of breeding population of Horned Puffins (Moe 1977). Large gulls (*Larus* spp.) and Common Ravens (*Corvus corax*) prey on chicks in nests (Amaral 1977, Wehle 1980). Impacts of introduced predators discussed in Conservation and management, below.

BREEDING

PHENOLOGY

Wehle (1980) distinguished 4 events upon arrival at breeding colonies: arrival in vicinity of colony; first visits to colony; establishment of continuous occupancy; initiation of egg-laying. Pre-egg stage lasts about 3 wk. There is a negative correlation between time of arrival and latitude. Birds arrive ≥1 mo later at northern breeding colonies than southern colonies

(see Migration, above). Time of arrival at individual colony is relatively constant among years; usually within same 1- to 2-wk period each year (Wehle 1980).

Pair formation and nest occupation. Mates arrive at breeding grounds in pairs or form pairs shortly after arrival. Occupy nesting habitat about 1 wk after arrival, typical of all puffin species (Swartz 1966, Sealy 1973, Wehle 1976, Amaral 1977).

Laying of eggs. In general, lays egg earlier at lower latitudes than high latitudes. Timing probably related to delay in food production and accessibility of nesting habitat as one goes north (Wehle 1980). In Gulf of Alaska, lays in mid- to late Jun (Fig. 3). On south-ernmost nesting colony, Forester I., lays in late Jun (Sealy 1973). Barrens (Amaral 1977): lays 14–20 Jun. Chisik I. (Jones and Petersen 1979): lays 5–29 Jun, with 66% of eggs 10–23 Jun. Ugaiushak (Wehle 1980): lays 4–14 Jun. Semidi Is. (Hatch and Hatch 1990a): first eggs 10–13 Jun, peak 15–25 Jun; mean of 7 yr, 21 Jun. Big Koniuji I. and Hall I. (Shumagin Is.; Moe and Day 1977): lays 18 Jun–4 Jul. Buldir I. (Wehle 1980): lays 13–20 Jun. Talan I. (1987–1989): First egg 7 Jun; peak laying 20–30 Jun, last eggs early Jul. In n. Bering Sea, lays egg mid-Jun through first week of Jul (Sealy 1973). On St. Lawrence I., lays 21–29 Jun. On Pribilofs (Sealy 1973), 19 Jun–1 Jul.
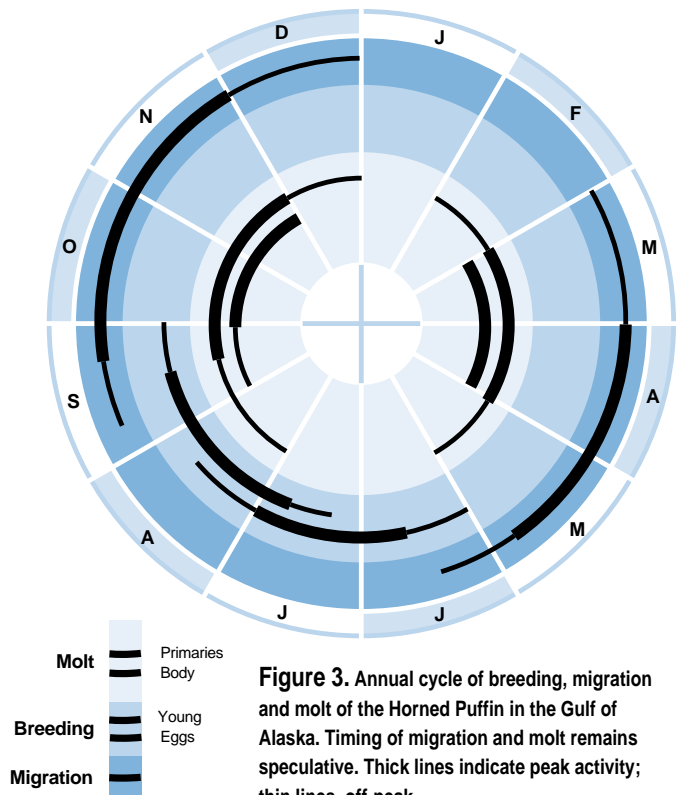
Hatching of eggs. Barren Is. (Amaral 1977): hatch 22–31 Jul. Chisik I. (Jones and Petersen 1979): Hatching began 18 Jul, 66% hatched 19–26 Jul. Ugaiushak (Wehle 1980): 25–30 Jul hatching. Big Koniuji and Hall I. (Shumagin Is.; Moe and Day 1977): hatch 28 Jul–14 Aug. At Buldir I. in 1988–1989, 82% of chicks hatched 19 Jul–5 Aug (Byrd and Douglas 1990); in 1976, hatch 21–30 Jul (Wehle 1980). Talan I. (1987–1989): first chicks 18 Jul, peak hatch 20–30 Jul, last chicks hatched 9 Aug.

Fledging and departure from colony. Chisik I. (Jones and Petersen 1979): fledging 28 Aug–19 Sep. Big Koniuji and Hall I. (Shumagin Is.; Moe and Day 1977): estimated fledging 4–27 Sep. Buldir I. (Byrd et al. 1989): fledging after 5 Sep. Talan I. (1987–1989): first fledglings 27 Aug, peak 10–20 Sep, last chicks fledged early Oct.

NEST SITE

Selection. No information.

Microhabitat; site characteristics. In contrast to other puffins, most common nesting habitat for Horned Puffin is rock crevices in talus and among beach boulders; typical habitat on St. Lawrence I. (Sealy 1973), Buldir I. (Wehle 1980), Cape Thompson (Swartz 1966), Chisik I. (Jones and Petersen 1979), and Big Koniuji I. (Moe and Day 1977). Also use cracks and crevices in cliff faces at most colonies, but densities low owing to nature of this habitat. Horned Puffins nest in earthen burrows at Suklik I. (Semidis; Hatch and Hatch 1990b), Chamisso I. (Nelson and Sowls 1985), and Castle Rock (Moe and Day 1977). The

Figure 3. Annual cycle of breeding, migration and molt of the Horned Puffin in the Gulf of Alaska. Timing of migration and molt remains speculative. Thick lines indicate peak activity; thin lines, off-peak.

Suklik I. colony is dense, and is the largest known Horned Puffin colony in Alaska. Nests at sea level to >300 m elevation in some colonies. On 13 plots ex-amined at Suklik in 1992 (ASK), 70 earthen burrows were found, 54 (74%) occupied; average density 1.08 burrows/m^2, and 0.831/m^2 for occupied burrows only. At Talan I., most nests situated in talus, combined talus/earthen burrows, and among beach boulders. Also, nests situated in combined earthen burrow/rock-crevice habitat among Japanese pine (*Pinus pumela*); average density 0.15 burrows/m^2 ± 0.06 SE (ASK). At Chisik I. (Jones and Petersen 1979), average density in beach boulder, talus, and talus/burrow habitat 0.18/m^2 ± 0.04 SE (range 0.04–0.44).

NEST

Construction process. Using feet and occasionally bill, excavates or clears crevices or burrows of soil, debris, feces, or mud. Nesting materials (dry grass, small twigs, and feathers) collected in vicinity of nests or at sea (along with algae and other floating materials, including scraps of plastic line and net). Brings nest materials to nest held cross-wise in bill. Amount of nest material varies from well-built nests with defined cup to few straws on floor of rock crevice. Unknown which sex builds nest.

Structure and composition matter. Of 16 crevice nests examined on St. Lawrence I., all contained dry grass; 1 had dry grass and feathers (Sealy 1973). Of 9 nests on Balka I. (Chukchi Peninsula), 8 contained

large feathers and dry grass, 1 had dry grass only (Portenko 1973).

Dimensions. No information.

Microclimate. At Ugaiushak (Wehle 1980): Temperature of burrow substrate at arrival, 2.1°C (range 0–4°C, *n* = 65); at egg-laying, 9.0°C (range 9.0–10.5°C, *n* = 23); hatching, 14.5°C (range 13–15.5°C, *n* = 4).

Maintenance or reuse of nests, alternate nests. Same nests usually occupied year after year; likely by same birds (Wehle 1980, Harris 1984). At Chisik I., of 11 birds banded in 1998, 5 were resighted breeding in same burrows in 1999 (A. Harding and JFP unpubl.). Alternate nests not known to occur.

EGGS

Shape. Elliptical or subelliptical. Shell is thick, roughly granulated (Sealy 1973).

Size. In contrast to adult body size, average length (65–69 mm), breadth (45–47 mm), and volume (133–147 ml) of eggs vary little among geographic regions. Forrester I.: mean length 66.8 mm ± 1.32 SD (*n* = 14) × mean breadth 46.0 mm ± 1.10 SD (*n* = 14; Willett 1913–1920 unpubl., provided by L. Kiff, Western Foundation of Vertebrate Zoology). Ugaiushak I.: mean length 66.9 mm ± 2.71 SD (*n* = 53) × breadth 45.7 mm ± 1.29 SD (*n* = 53; Wehle 1980). Buldir I.: mean length 66.2 mm ± 2.59 SD (*n* = 19) × breadth 45.8 mm ± 1.29 SD (*n* = 19; Wehle 1980). Chamisso I.: mean length 67.3 mm (*n* = 20), mean breadth 46.0 mm (*n* = 20; Grinnell 1900). Talan I.: mean length 67.4 mm ± 0.27 SD (*n* = 91), mean breadth 45.9 mm ± 0.14 SD (*n* = 91; ASK). Second eggs produced are about 9% smaller in volume than first (Wehle 1980).

Mass. Average mass of eggs about 73–79 g from various collections. Ugaiushak I.: mean mass 75.1 g ± 5.13 SD (*n* = 53; Wehle 1980). Buldir I.: mean mass 76.2 g ± 4.75 SD (*n* = 18; Wehle 1980). Talan I.: mean mass 75.9 g ± 0.68 SD (*n* = 78; ASK). Mass of known fresh eggs: 75.9 g ± 0.68 SE (*n* = 78; Talan I.; ASK). Mass loss during incubation: 17.6 g ± 0.83 SE, or about 23% (*n* = 39; Talan I.; ASK). Wehle (1980) estimated a loss of about 12% (*n* = 9) during incubation. Mass of egg in proportion to female body mass: 14.4–15.8% (Wehle 1980).

Color. Dull white, dirty white, or creamy white. May show faint markings, spots, or scrawls of pale lavender-gray or pale olive on buff (Sealy 1973). Some have few dark brown spots and scrawls (Portenko 1973). Eggs become soiled during incubation.

Eggshell thickness. No information.

Clutch size. One. See also Demography and populations: measures of breeding activity, below.

Egg-laying. Little known. Replacement eggs may be laid if first are lost (Wehle 1980).

INCUBATION

Onset of broodiness and incubation in relation to laying. Incubation starts shortly after egg-laying.

Incubation patches. Two lateral brood patches present in both sexes (Sealy 1973). Average size (Wehle 1980): 57.4 mm ± 8.45 SD × 23.1 mm ± 2.87 SD (*n* = 19). Defeathering begins several days before egg-laying, similar size brood patches. Signs of refeathering at end of incubation, but only a few birds attained complete refeathering during mid-chick–rearing.

Incubation period. Mean 40.2 d (range 39–42 d for 2 nests) at Barren Is. (Amaral 1977). Mean 41.1 d (range 40–43, *n* = 5) at St. Lawrence I. (Sealy 1973). Mean 41.2 d ± 3.4 SD (*n* = 20) from Gulf of Alaska (Petersen 1983). Mean 39.6 d ± 0.53 SE (range 38–45, *n* = 15) at Talan I. (ASK). Incubation temperature 38°C (*n* = 3; Sealy 1973).

Parental behavior. Little known. Both sexes incubate. Egg can be left unattended several hours to a day, incubated up to a day or more by same individual without incubation exchange (Wehle 1980). Adults may exchange incubation duties mostly during early evening (Amaral 1977).

Hardiness of eggs against temperature stress; effect of egg neglect. No quantitative information. Eggs can be left unattended for several hours a day, or even entire day, with little apparent effect (Wehle 1980). Eggs laid directly on ice hatched successfully (ASK).

HATCHING

Preliminary events and vocalizations. Chick starts producing sounds after pipping. If exposed to low ambient temperature, chick produces long "*uiiiep*" distress call.

Shell-breaking and emergence. Few data (Wehle 1980). Days from first cracks to hatching, mean 3.0 d (range 2–4, *n* = 2); from first cracks to pipped, 4.0 d (*n* = 1), from pipped to hatching, 3.5 d (range 3–4, *n* = 2).

Parental assistance and disposal of eggshells. Eggshells usually pushed out of nest chamber, but sometimes left in nest.

YOUNG BIRDS

Condition at hatching. Semiprecocial chick, covered with long downy feathers, eyes opened, white egg tooth. After day 6, hatchling can maintain body temperature (39.5°C; Sealy 1973). Hatchling measurements at Talan I.: mass 47.9 g ± 1.02 SE (*n* = 15); culmen 18.9 mm ± 0.22 SE (*n* = 18); tarsus 20.7 mm ± 0.25 SE (*n* = 18). At St. Lawrence I. for 1-d-old chick (*n* = 2): mass, 58.6 g; culmen, 17.2 mm; tarsus, 19.3 mm (Sealy 1973). At Barren Is. for 1-d-old chick: mass, 54.3 g (*n* = 3); wing length, 25 mm; culmen, 17.6 mm; tarsus, 25.6 mm (*n* = 3; Amaral 1977). Egg tooth present on upper bill until 15–28 d of age (Amaral 1977); most fall off within 14 d, sometimes 1–4 d (Wehle 1980).

Growth and development. Chick growth and development highly variable, reflecting intermittent provisioning by parents (Kitaysky 1996). Consequently, growth rates range widely among studies, from low of 3.4 g/d at Semidi Is. to 13.4 g/d at Barren Is.

(Amaral 1977, Petersen 1983). Other values: Buldir I., 8.2 g/d (n = 14) and 9.4 g/d (n = 6; Byrd and Douglas 1990); Barren Is., 10.1 g/d (Manuwal and Boersma 1977); Chisik I., 10.7, 12.8, and 9.4 g/d (Jones et al. 1980, Slater et al. 1995); Ugaiushak I., 10.9 g/d (Wehle 1980); Shumagin Is., 12.6 g/d (Moe and Day 1977); Semidi Is., 5.7 g/d (Petersen 1983); St. Paul I., 12.0 and 11.5 g/d (Hunt et al. 1982). Overall average chick growth rate from above 13 colony-years of study: 10.0 g/d ± 4.6 SD.

Chick developmental rate depends on daily food intake (Kitaysky 1999). Maximal body mass growth rates of captive chicks fed *ad libitum* (108 g/d) were 11.2 g/d ± 0.54 SE, higher than in chicks fed 63 g/d (7.63 g/d ± 0.74 SE) and 53.0 g/d (6.45 g/d ± 0.46 SE). Similarly, rates of skeletal development were highest among chicks fed *ad libitum* (culmen, 0.32 mm/d ± 0.023 SE; tarsus, 0.45 mm/d ± 0.018 SE) and slowest among chicks fed 53.0 g of food daily (culmen, 0.23 mm/d ± 0.015 SE; tarsus, 0.25 mm/d ± 0.02 SE). Development of remiges followed same pattern: highest in *ad libitum*-fed birds (primaries, 2.05 mm/d ± 0.045 SE; secondaries, 1.24 mm/d ± 0.043 SE) and lowest among chicks fed 53 g of food daily (primaries, 1.65 mm/d ± 0.062 SE; secondaries, 1.00 mm/d ± 0.076 SE). High variation in chick developmental rates related to ability of chicks to adjust metabolic rate to food provisioning (Kitaysky 1996). Hungry chicks can decrease metabolic rate by 46.8%, providing substantial energy economy during food shortages.

PARENTAL CARE

Brooding. Parents brood chick for 6–7 d after hatch (Amaral 1977, Wehle 1980). Both parents participate. Brooding terminated after chicks can thermoregulate (Wehle 1980).

Feeding. Both sexes feed young during daylight hours. At Barren Is., first deliveries started at 05:00 and peaked at 05:00–08:00 in morning and 17:00–21:00 in evening. Two peaks in feeding at Buldir I., one early to mid-morning and one late afternoon to early evening (Wehle 1980). In late chick-rearing, fed throughout day with several peaks of activity. Adults delivering food spend little time in burrow and leave within 1 min after arrival. Chick-provisioning rates reflect abundance of food resources, which vary considerably from day to day (Kitaysky 1996).

Adults delivered 2–6 meals/d to chicks at Barren Is. (Manuwal and Boersma 1977). At Chisik I., adults delivered 3.0 meals/d ± 1.0 SD (range 1–5, n = 19) in early to middle chick-rearing in 1997 and 6.1 meals/d ± 2.1 SD (range 3–9, n = 10) during late chick-rearing in 1996 (A. Harding and JFP unpubl.). Given average meal-load sizes of 14.9 and 16.4 g/load during these periods in 1996 and 1997, respectively, chicks were fed about 48 g/d in early to middle chick-rearing and 90.9 g/d during late chick-rearing. These are similar rates of delivery to those observed (Kitaysky 1996) at

Talan I. in 1987 (41 g/d), and to amount eaten *ad libitum* by Horned Puffin chicks in captivity (about 90 g/d). Rates of delivery highly variable; days may pass between feedings, followed by days with much higher than average meal loads (Kitaysky 1996). More study needed to establish feeding rates and patterns of delivery at colonies. By comparison, 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 in 1 d (Harris 1984). Tufted Puffins deliver an average of 4.1 meals/d (range 1.9–6.2, n = 12 colony-years; Piatt et al. 1997, JFP, T. van Pelt, and S. A. Hatch unpubl.), and this can vary considerably among years at the same colony.

Nest sanitation. Incubating birds leave nest chamber for defecation. Chicks defecate close to nest entrance or in tunnels to side of main nest chamber.

COOPERATIVE BREEDING

Not known in this species.

BROOD PARASITISM

Not known in this species.

FLEDGLING STAGE

Departure from nest. Departs nest at dusk and during night by flying or walking from nests directly to open water. Fledglings dive immediately upon hitting water and swim rapidly away from colony (JFP).

Period from hatching to departure. Range of nestling periods reported in Wehle 1980 for several studies with small sample sizes: 34–43 d. Nestling period from Gulf of Alaska: 42.3 d ± 0.85 SE (range 37–46, n = 12; Petersen 1983). Daily rates of food intake affect duration of fledgling period (Kitaysky 1996): *ad libitum* chicks in captivity reached fledging conditions within 44.7 d ± 1.2 SE; captive chicks that received 53 g of food daily developed to fledging conditions within 55.5 d ± 1.0 SE.

Growth. Substantially smaller than adult at fledging in most measurements (e.g., mass and culmen 66% of adult; Table 1), but tarsus fully developed. Plumage fully developed, but feathers only 75–85% size of adult, wing-chord 84%. While fledgling period and fledging body mass can vary markedly among colonies, and within and among years, development of wings and feathers fairly constant (Kitaysky 1996). Peak mass prior to fledging reported for 2 yr at Semidi Is. 280, 291 g (Petersen 1983); 2 yr at Barren Is. 440, 445 g (Amaral 1977, Manuwal and Boersma 1977); Chisik I. 400 g (Jones et al. 1980); Shumagin Is. 405 g (Moe and Day 1977), Ugaiushak I. 380 g (Wehle 1980). Fledging mass from Talan I. 349, 341, 354 g in 1987–1989, respectively (Kitaysky 1996).

Association with parents or other young. Little information. Adults do not accompany chicks at sea or provide postfledging parental care (Wehle 1980, ASK).

Table 1. Linear measurements (mm) and mass (g) of Horned Puffins at Talan I. (ASK). Data shown as mean ± SE (*n*).

	Chick at hatching	Chick at fledging	Breeding adult
Mass	47.9 ± 1.02 (15)	348.7 ± 3.17 (76)	520.9 ± 5.99 (67)
Culmen	18.9 ± 0.22 (18)	31.8 ± 0.19 (74)	48.3 ± 0.28 (67)
Tarsus	20.7 ± 0.25 (18)	30.2 ± 0.13 (74)	30.7 ± 0.23 (68)
Wing-chord	19.2 ± 0.11 (15)	156.9 ± 0.55 (76)	187.9 ± 0.80 (68)
P10 remiges		86.8 ± 0.54 (22)	111.5 ± 2.75 (3)
S2 remiges		52.7 ± 0.52 (22)	58.3 ± 2.85 (3)
Back-feathers		33.9 ± 0.70 (22)	41.0 ± 1.53 (3)
Belly-feathers		29.6 ± 0.44 (22)	32.7 ± 0.88 (3)
Tail-feathers		50.1 ± 0.70 (22)	65.5 ± 0.69 (67)

Ability to get around, feed, and care for self. Little information. Can fly poorly, dives and swims well.

IMMATURE STAGE

Little information. Immatures apparently move to central North Pacific for 1–2 yr before return to breeding areas (see Migration, above). A captive chick (JFP) grew at rate of 10.5 g/d to peak mass of 375 g, fledged at about 45 d (based on behavior and weight recession), then entered a phase of linear growth (2.6 g/d) between 45 and 90 d, followed by a slower phase of linear growth (1.7 g/d) between 90 and 140 d, when it reached adult mass (530–540 g). Two captive Tufted Puffin chicks exhibited similar growth patterns.

DEMOGRAPHY AND POPULATIONS

MEASURES OF BREEDING ACTIVITY

Age at first breeding. No data. May be similar to Atlantic Puffin; i.e., sometime in third or fourth year, but most not until fifth year (Harris 1984).

Clutch. One egg. Replacement may be laid 16–20 d after loss of first egg; possibility of second replacement egg (Wehle 1980). Old reports of 2-egg clutches (Dement'ev and Gladkov 1951) have never been confirmed. Because adults develop 2 lateral brood patches, it has been suggested that 2-egg clutches occurred in evolutionary history (Wehle 1980).

Annual and lifetime reproductive success. No information on lifetime reproductive success. Annual reproductive success (number of chicks fledged/egg laid) varies among years and locations (Appendix 3). Over all colony-years of study (*n* = 43), average hatching success 75%, fledging success 73%, and reproductive success 0.56 chicks/pair. These figures do not account for varying proportion of birds that attempt to breed (laying success). Most data obtained at 4 sites (Chisik, Semidi, Buldir, and Talan Is.). Remarkably low variability in breeding success within and among

sites: Chisik I., mean 0.56 ± 0.17 SD (*n* = 8, Coefficient of Variation [CV] 30%); Semidi Is., mean 0.59 ± 0.16 SD (*n* = 7, CV 28%); Buldir I., mean 0.47 ± 0.11 SD (*n* = 11, CV 24%); Talan I., mean 0.57 ± 0.20 SD, *n* = 8, CV 35%. Variability probably related to fluctuations in food supplies and correlated with oceanographic conditions (Kitaysky and Golubova 2000).

Reproductive success affected at each stage of breeding. Eggs may fail to hatch from infertility, predation, or rolling out of nest site (Wehle 1980, Petersen 1983). Chicks may die from predation or starvation at nest site, often precipitated by lack of attendance by adults owing to food shortage (Wehle 1980). Chicks vulnerable to predation near fledging stage as they become more active and leave security of nesting crevice or burrow (Amaral 1977). Chicks vulnerable to mortality by exposure to cold, wet weather (Amaral 1977, Petersen 1983) particularly before endothermy is achieved at about 6 d (Sealy 1973). Chicks that survive past 2 wk usually survive to fledging as long as adults are capable of feeding (Wehle 1980).

Number of broods normally reared per season. One.

LIFE SPAN AND SURVIVORSHIP

Little information. Individuals marked on Buldir I. in 1970s were observed in 1990s, suggesting that some may survive >20 yr (Gaston and Jones 1998).

DISEASE AND BODY PARASITES

Horned Puffins host a number of helminthic parasites, but none known to cause morbidity or mortality. Parasitological studies conducted across geographic range for this alcid (reviewed in Hoberg 1992a, 1996). Intestinal parasites such as tapeworms are common, represented by species of *Tetrabothrius* (2 or 3 species) or *Alcataenia* (3 species). Only *A. fraterculae* is widely distributed and a host-specific parasite occurring from Okhotsk Sea across North Pacific basin (Hoberg 1986). Tapeworms in Horned Puffins and alcids have been focus of studies in cospeciation and historical biogeography for North Pacific (Hoberg 1986, 1992b).

Although 5 species of trematodes reported, flatworms other than *Pseudogymnophallus alcae* in gall bladder and perhaps *Renicola* in kidneys appear uncommon. Nematodes represented by species of *Contracaecum* in proventriculus, and *Seuratia* and *Stegophorus* in gizzard, whereas acanthocephalans are incidental parasites.

Ectoparasites also known to infest Horned Puffins, but no definitive studies conducted (Hoberg and Wehle 1982). Phthiraptera (lice), including *Saemundssonia fraterculae* and *Quadraceps* sp., are known from several localities in North Pacific and Bering Sea. The ubiquitous tick *Ixodes uriae* probably occurs with Horned Puffins and other seabirds throughout breeding ranges.

CAUSES OF MORTALITY

Causes of adult mortality include predation (see Behavior: predation, above), starvation, and human factors such as oil pollution, net mortality, and harvest (see Conservation and management: effects of human activity, below). Nothing known away from colonies about adult or subadult mortality. Emaciated individuals often wash ashore in winter, suggesting starvation at sea not uncommon (Roberson 1980, Clapp 1986).

RANGE

Natal philopatry. No information.

Fidelity to breeding site and winter home range. Fidelity to breeding site well established in Tufted and Atlantic puffins (Wehle 1980, Harris 1984). At Chisik I., of 11 Horned Puffins banded as breeders in 1998, 5 were resighted and breeding at the same nest sites in 1999 (A. Harding and JFP unpubl.).

Dispersal from colony. No information.

Home range. See Food habits: feeding, above.

POPULATION STATUS

Numbers. Population estimates are unreliable owing to difficulty of censusing birds in crevice- and burrow-nesting habitat. No standardized census methods developed. Some estimates from count of birds on water. Most estimates based on observations of birds attending colonies, but ratio of birds attending at any given time to local population unknown.

Most significant colonies in North America and Russia have been located (829 known colonies; see Table 2; Sowls et al. 1978 [and updated U.S. Fish Wildl. Serv. Computerized Seabird Colony Catalog 1999], Shuntov 1986, Byrd et al. 1993, Konyukhov et al. 1999). Total world colony population estimate is 1,088,500 individuals, of which 86% (939,750) breed in North America. Small proportion of North American population in British Columbia (<0.1%), se. (<1%) and s.-central (1.4%) Alaska. Largest colonies concentrated in nw. Gulf of Alaska along Alaska Peninsula on Semidi, Shumagin, and Sanak Is., which account

for 80% of North American population (Sowls et al. 1978, Byrd et al. 1993). North American population scattered throughout Aleutian Is. (10%) and in Bering (7%) and Chukchi (2%) Seas.

Populations can also be estimated from densities of birds at sea (Piatt and Ford 1993). For 10 common species of seabirds in Alaska for which both colony and pelagic estimates are available, correlation (r^2 = 0.94) between both types of population estimate is quite good but poorest for Horned Puffins; linear regression suggests that colony counts have overestimated Horned Puffin populations about threefold (see Fig. 3 in Piatt and Ford 1993). On the other hand, pelagic estimates of Horned Puffin may be conservative compared to other species because a substantial number of subadult and nonbreeding individuals may summer in the central North Pacific (see Distribution, above). Further, colony counts and pelagic estimates may enumerate different populations—those at sea being different from those attending colonies (since at least during incubation, one bird remains at colony). We conclude that the North American population stands at about 1 million birds.

The 628 known colonies in North America are widely distributed, but only 21 colonies contain >5,000 individuals, and these may account for >83% of the North American population, most (80%) of which is found along the Alaska Peninsula. Median size of colonies is only 48 birds, however, and it seems likely that populations at many large colonies have been grossly overestimated. Nonetheless, important colonies are indicated from large population estimates: Suklik I., 250,000; Amagat I., 140,000; Big Koniuji I., 63,000; Aghik I., 60,000; Castle Rock, 60,000; Chowiet I., 35,000; St. George I., 28,000; Near I., 20,000; Buldir I., 20,000 (but may be >100,000; I. L. Jones pers. comm.); Ugaiushak I., 18,200; High I., 18,000; Davidof I., 11,600; Puffin I., 10,000; and Kateekuk I., 10,000. The situation is similar in Russia, where only 15 colonies account for 95% of population estimate, and only 2 colonies (Talan I., 100,000; Matykil I., 17,500) account for 84%, while median (n = 201) colony size is only 10 birds (USFWS Computerized Seabird Colony Catalog 1999, JFP).

Frequency of occurrence of colonies may provide a better indication of population distribution (Table 2). This still indicates that Gulf of Alaska is center of abundance (60% of colonies) for Horned Puffins in North America, but suggests higher proportion of North American population is found in the Aleutians (21%) and in the Bering/Chukchi Seas (19%).

Trends. Boat-based censuses of seabirds at sea in Prince William Sound suggest a 59% decline from 3,580 individuals (3,055 95% C. I.) in 1972 to 1,481 (1,223) in 1989–1993 (Agler et al. 1999); and a further 50% decline to 746 (500) in 1996–1998 (Lance et al. 1999); for an overall 79% decline from 1972 to 1998.

Table 2. Horned Puffin colonies and populations in the North Pacific. Compiled from Seabird Colony Atlas for Alaska and Russia, U.S. Fish Wildl. Serv., Anchorage.

	Number of colonies	Number of individuals	Percentage of colonies	Percentage of individuals
Gulf of Alaska				
British Columbia	11	50	1.3	0.0
Se. Alaska	15	270	1.8	0.0
N. Gulf of Alaska	91	12,830	11.0	1.2
E. Alaska Peninsula	197	408,640	23.8	37.7
W. Alaska Peninsula	64	339,640	7.7	31.3
Total Gulf of Alaska	378	761,430	45.6	70.2
Aleutians				
E. Aleutians	61	7,170	7.4	0.7
Central Aleutians	43	22,860	5.2	2.1
W. Aleutians	27	61,060	3.3	5.6
Total Aleutians	131	91,090	15.8	8.4
Bering/Chukchi Seas (U.S.)				
S. Bering Sea	26	37,110	3.1	3.4
N. Bering Sea	68	32,840	8.2	3.0
Chukchi Sea	25	17,280	3.0	1.6
Total Bering/Chukchi Seas	119	87,230	14.4	8.0
Total North America	628	939,750	75.8	86.7
Russia				
Chukchi Sea	13	2,140	1.6	0.2
N. Bering Sea	93	21,150	11.2	2.0
S. Bering Sea	66	6,130	8.0	0.6
Sea of Okhotsk	29	119,330	3.5	11.0
Total Russia	201	148,750	24.2	13.7
Total world	829	1,088,500	100.0	100.0

This paralleled a similar rate of decline for 14 other species of fish-eating seabirds in Prince William Sound and a 40% decline in Common Murre populations throughout the Gulf of Alaska between the 1970s and 1990s (Piatt and Anderson 1996). The decline of murres was correlated with major changes in food base for seabirds in the Gulf of Alaska, apparently the result of changing marine climate (Anderson and Piatt 1999). Fatty forage fish such as capelin essentially disappeared in the gulf and from diets of fish-eating seabirds, including Horned Puffins (Appendix 2; Piatt and Anderson 1996) and were replaced by less nutritious prey such as pollock and squid. Reduction in productivity and populations observed in Gulf of Alaska murres and other fish-eating seabirds (and marine mammals) probably applied to Horned Puffins as well.

Other information extremely limited. At Chisik I. (Cook Inlet), population may have declined >50% from crude, but repeated estimates of 5,000–6,000 individuals in 1971, 1978, 1979, and 1983 (Sowls et al. 1978, Jones et al. 1980, Slater et al. 1995) to an average

maximum count of 2,454 ± 1,136 individuals in 1995–1999 (A. Harding and JFP unpubl.). In 1900, Chamisso I. (Kotzebue Sound, Chukchi Sea) contained immense numbers (Grinnell 1900), and in 1946 this same colony was one of the largest of this species Gabrielson had seen (Gabrielson and Lincoln 1959); although he may have been referring to adjacent Puffin I. as well. Chamisso was first censused systematically in 1977, and estimated population (4,500 birds) declined by 38% by 1981 (2,800 individuals) and by a further 80% by 1987 (552 individuals) when recensused using same methods (Nelson and Sowls 1985, A. Sowls pers. comm.). At Cape Thompson (Chukchi Sea), counts of Horned Puffins at 5 colony areas changed little between 1960 (1,362 individuals; Swartz 1966) and 1976/1977 (1,359/1,072 individuals; Springer et al. 1985). In Russia, Horned Puffins increased from 100 birds in 1938 to 600–860 birds in 1985 at Kolyuchin I. (Kondratiev et al. 1987), and at Olyumka (Anadyr Bay; 1,500–2,000 birds), numbers have probably been stable since 1932 (Velizhanin 1987).

POPULATION REGULATION

Little known. As is true for other seabirds, puffins require predator-free nesting islands or mainland habitat and abundant supplies of food during breeding and nonbreeding seasons. Given wide distribution in Alaska, abundance of offshore islands, and generally small colony sizes, populations are probably not limited by breeding sites. Prey availability is likely most important source of population regulation, and nonlinear functional relationships between Atlantic Puffin population parameters and prey abundance are well described (Anker-Nilssen et al. 1997). No quantitative data available to demonstrate this for Horned Puffins.

CONSERVATION AND MANAGEMENT

EFFECTS OF HUMAN ACTIVITY

Hunting and harvest. Adults and eggs harvested for subsistence in some areas of Alaska, particularly in Bering Strait region. While tens of thousands of seabirds and eggs are harvested annually, focus is on accessible, aggregated species such as murres or auklets, and harvest of Horned Puffin is minimal and localized (Paige et al. 1996).

Toxic chemicals and oil pollution. No known studies of organochlorine or heavy-metal contamination of eggs or tissue. Vulnerable to oil pollution, but no estimate of chronic mortality; no major oil-mortality events reported. Most oil spills occur in winter when puffins are largely absent from Alaskan waters. Only 162 Horned Puffins were retrieved in aftermath of *Exxon Valdez* spill in Mar 1989, but most of these died from natural causes in late summer (Piatt et al. 1990a).

Ingestion of plastics. Plastic particles are frequently found in gizzards: 37% of 268 individuals examined from subarctic Alaska between 1969 and 1990 (Robards et al. 1995) and 57% of 57 birds examined from central North Pacific in 1990–1991 (Robards et al. 1997). Plastics ingested have been of 2 main types: industrial pellets (40%) and user plastics (60%; fragments of containers, toys, etc.). Plastic pollution and ingestion, widespread throughout the subarctic Pacific, increased between the 1970s and 1990s (Robards et al. 1995, 1997). Plastics potentially could obstruct passage of food or affect physiology, but detrimental effects have not been demonstrated.

Fishing nets. Bycatch in gill nets widespread in North Pacific. From 1950s to 1990s, tens of thousands killed in offshore salmon and squid drift-net fisheries (DeGange et al. 1993). Squid drift-net fisheries alone killed an estimated 49,000 (± 53,000 95% Confidence Limits) Horned Puffins annually during 1980s (De-Gange et al. 1993). Catches declined to <1,000 individuals by 1990 (Johnson et al. 1993) because high-seas drift-net fisheries were largely eliminated. Coastal gill-net fisheries continue to catch birds in Alaska, Russia, and Japan, but magnitude of bycatch is probably small compared to high-seas bycatch (DeGange et al. 1993).

Introduced mammals. Mammalian predators were once absent from most islands in the Northeast Pacific, but arctic fox (*Alopex lagopus*), red fox (*Vulpes vulpes*), Norway rats (*Rattus norvegicus*), and ground squirrels (*Spermophilus undulatus*) were intentionally or accidentally introduced into many seabird colonies in Alaska during the 1800s and early 1900s. These predators decimated or eliminated seabird populations on many islands, although Horned Puffins were less affected because they usually nest in less accessible crevices (Bailey and Kaiser 1993).

Disturbance at nest and roost sites; direct human/research impacts. Investigator disturbance during incubation or hatching may cause desertion (Amaral 1977, Wehle 1980); less of a problem than for Tufted Puffins because crevice habitat less vulnerable to destruction than burrows (Byrd et al. 1993). In Atlantic Puffins (Rodway et al. 1996) and crevice-nesting auklets (Piatt et al. 1990b), higher frequency of visitation to individual nest sites can reduce breeding success and degrade nesting habitat.

MANAGEMENT

Other than eradication of introduced predators (see above), which benefits all seabirds and Horned Puffins indirectly, no management programs for this species. Owing to difficulties in censusing, and lack of standardized methods, Horned Puffin populations are not routinely monitored by U.S. Fish and Wildlife Service (USFWS) anywhere in Alaska (Byrd et al. 1993). Most colonies, and all large colonies, are protected within USFWS National Wildlife Refuge (NWR) system; in particular, by Alaska Maritime NWR.

APPEARANCE

MOLTS AND PLUMAGES

Sexes alike in all plumages. Timing and duration of molt poorly known (Fig. 3). Two molts a year. Nothing known about molt in subadults. Following descriptions of molt and plumage are largely from Dement'ev and Gladkov 1951 and Kharitonov 1990.

Hatchlings. Completely downy, uniformly black with pure or silver-white belly. Black "horn" is well developed, legs and beak are brownish. Down is longer on upperparts, wings, and top of head; short and dense on underparts; short and thin around eyes and base of bill.

Juvenal plumage. Feather development known from studies on Talan I. (ASK). Primary and secondary remiges emerge as pin-feathers at average of 9–10 d (range 5–18), and burst from sheaths at 16 d (range 12–24). Tertials, back, and belly pins erupt at 8–9 d

(range 4–18), and feathers erupt at 13–15 d. Tail pins emerge at 18 d (range 15–22) and feathers at 21 d (range 16–24).

Juvenal plumage similar to Definitive Basic plumage, fully developed at departure from nest; down sometimes remains on nape and rump.

Basic I plumage. Prebasic I molt complete; molt occurs early, perhaps Jul–Aug (Dement'ev and Gladkov 1951). Molt sequence unknown.

Basic I plumage similar to Definitive Basic. Lores and sides of head above and behind eye are charcoal gray or black. Middle of throat and foreneck are grayish black.

Alternate I plumage. Immatures undergo Prealternate I molt in Feb through Apr of their second calendar year (JFP, observations of captive bird). Molt sequence unknown. Alternate I plumage similar to Definitive Alternate plumage except cheeks are grayish.

Definitive Basic plumage. Definitive Prebasic molt complete; occurs postbreeding (Oct–Nov). Molt sequence unknown.

Lores, anterior cheeks, and sides of forehead charcoal gray, narrow black stripe extends posteriorly behind eye, remainder of cheeks grayish white. Remainder feathering same as Definitive Alternate plumage.

Definitive Alternate plumage. Definitive Prealternate molt partial; occurs late winter–early spring; molt sequence unknown.

Forehead, crown, nape, sides of neck, chin, throat, uppermost breast, back, scapulars, rump, upper tailcoverts, wings, and tail black, becoming brownish on forehead and dark grayish on chin. Remaining upperparts often tinged brownish. Blackish portions of head contrast with large white facial-patch, which extends from base of upper mandible back through ear-coverts to side of upper neck, up over eye to supraloral region and down to commisure. White patch somewhat rectangular in shape, but rear portion ends on side of neck in a point. Narrow blackish stripe extends from eye back through white patch to pointed rear end of patch. Remainder of breast and remaining underparts white except blackish-brown stripe along rear portion of thigh connects with ring of similar color encircling bottom of thigh where thigh-feathers terminate. Underwing surface charcoal gray to brownish gray, becoming black along leading edge of wing.

BARE PARTS

Bill and gape. Bill large, triangular, and laterally compressed. In Definitive Alternate plumage, basal two-thirds of bill yellow while distal third red, and a variable number (2–6) of vertical grooves or furrows present on distal third. Gape forms a fleshy, rictal rosette at corner of mouth that is bright yellow or orange in color.

In Definitive Basic plumage, part of the bill covering (ramphotheca) at base of upper mandible (where bill joins forehead) lost, reducing size and changing shape of bill. As a result, dorsal ridge of upper mandible (culmen) no longer forms a continuous curve with forehead, but base of culmen angles downward to forehead where portion of ramphotheca at base of upper mandible lost. Basal two-thirds of bill brownish while distal third orange-red with a few grooves. Rictal rosette also absent.

Bill in Juvenal and Basic I plumages is less deep than in Definitive Basic plumage (with less arched culmen), lacks grooves on culmen, and is brown in color. By Alternate I plumage, rictal rosette in gape and basal ridge of culmen begin to develop, but are smaller than in adults.

Iris. Light brown to brownish gray.

Bare skin on head. In Definitive Alternate plumage, orbital ring is red with a prominent fleshy, long, narrow, black "horn" up to 12 mm in length that extends upward from eye. In Definitive Basic plumage, "horn" is absent, and orbital ring is brown. Orbital ring blackish in Basic I plumage; "horn" not present in Juvenal plumage or Basic I plumage.

Legs, toes, and webs of feet. Yellowish orange to red in Definitive Alternate plumage, pale tan or flesh color in Definitive Basic plumage, and black in juveniles and Basic I plumage. Inner toe turned inward, more sharply hooked than others.

MEASUREMENTS

LINEAR

Sexual dimorphism has been suggested (Sealy 1973), but not established. Geographic variability not previously described. However, data compiled on live or freshly collected specimens (Appendix 4) and skeletal measurements (Appendix 5) reveal both sexual and geographic variability in body-size measurements.

Considering data from all sources combined, males significantly ($p < 0.01$) larger than females in bill length (mean male 49.6 mm ± 2.4 SD [$n = 90$]; mean female 47.4 mm ± 1.9 SD [$n = 91$]), bill depth (mean male 41.9 mm ± 2.6 SD [$n = 30$]; mean female 40.3 mm ± 1.9 SD [$n = 27$]), tarsus length (mean male 31.3 mm ± 1.9 SD [$n = 62$]; mean female 30.3 mm ± 1.6 SD [$n = 58$]), and wing length (flattened wings only: mean male 191.4 mm ± 5.5 SD [$n = 78$]; mean female 187.3 mm ± 6.2 SD [$n = 76$]). Bill width data known only from w. Alaska Peninsula (21 males, 8.02 mm ± 0.9 SE; 17 females, 7.85 mm ± 1.3 SE; JFP). Measurement of skeletal characteristics (principally along Alaska Peninsula) offers more precise data on sexual dimorphism: Males significantly larger than females in 16 of 20 skeletal measurements (Appendix 5).

Bill length in both males ($p < 0.05$) and females ($p < 0.001$) varied significantly (using ANOVA) among study areas. Wing lengths of males ($p < 0.001$) and
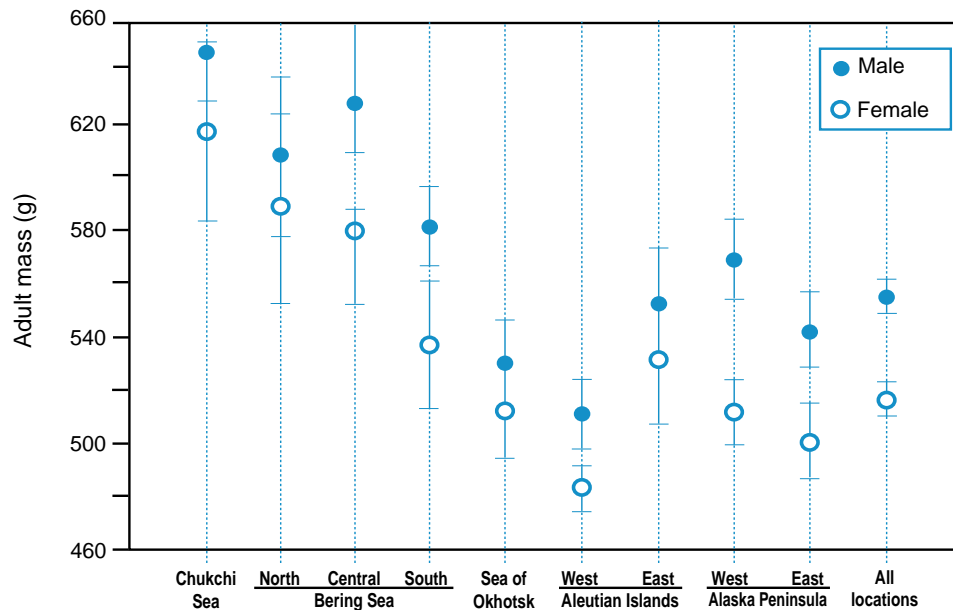
Figure 4. Geographic variation in body mass of the Horned Puffin.

females ($p < 0.001$) also varied significantly among study areas. (Wing lengths reported from St. Lawrence and Pribilof Is. were wing-chord measures, whereas all others were flattened wing lengths. These 2 sites were excluded from statistical analysis and would likely be 5+ mm longer if flattened.) Apparent clinal variation from north to south: individuals in Chukchi Sea (Cape Thompson) and Bering Sea (St. Lawrence I., Nunivak I., Pribilof Is.) larger than those in Sea of Okhotsk (Talan I.), Aleutians, or along Alaska Peninsula. East-west clinal variation as well. Wing measures (chord or flattened uncertain; S. Kharitonov unpubl.) of museum specimens from Chukotsk Peninsula (8 males: 192.8 mm ± 5.1 SE; 4 females: 190.5 mm ± 8.2 SE) and Komandorskiye Is. (4 males: 189.5 mm ± 4.1 SE; 5 females: 182.2 mm ± 3.2 SE) further support suggestion that birds are larger in Bering Sea than in Aleutians.

MASS

As is true for measurements, slight sexual dimorphism suggested previously (Sealy 1973) and geographic variability not described. Using compiled data (Appendix 4; Fig. 4), significant sexual dimorphism ($p < 0.001$) and geographic variability in mass was found for both males ($p < 0.001$) and females ($p < 0.001$; JFP and ASK). Overall, males (556.0 g ± 45.6 SD [$n = 210$]) were 7.5% heavier than females (517.2 g ± 44.6 SD [$n = 219$]). Mass of both sexes show pronounced north-south cline from heaviest (male 648 g, female 618 g) in Chukchi Sea to lightest (male 511 g, female 483 g) in w. Aleutians. Some east-west variability also, with birds from w. Alaska Peninsula (males 570 g, females 513 g) larger than those at similar latitude to west.

Some geographic variability in mass likely due to variability in timing of collections, as puffin mass can vary by 7–10% during breeding season (Sealy 1973, Barrett and Rikardsen 1992). However, mass varied among sites by >21% for males and females. As for Atlantic Puffins, Bergman's Rule may partially explain larger size at higher (colder) latitudes (Harris 1984), but not east-west variation. Geographic variability in marine production, coupled with variable chick development in relation to food intake, may also have a strong influence on body size (Kitaysky 1999).

Although no subspecies described, geographic variability in size of Horned Puffin mirrors that of Atlantic Puffin, which has 3 recognized subspecies (Harris 1984). *Fratercula arctica arctica* has widest range of average size (about 440–530 g) and distribution (Novaya Zemlya, Norway, Iceland, Newfoundland); *F. a. grabae* is smaller (about 370–410 g) and restricted to British Isles; *F. a. naumanni* larger (about 650 g) and found at high latitudes (Spitsbergen, Greenland). Thus, Horned Puffin overlaps considerably in body size with subspecies of its congener Atlantic Puffin.

PRIORITIES FOR FUTURE RESEARCH

In general, the biology of this species is poorly known, and basic studies of all kinds are needed to flesh out our understanding of Horned Puffin ecology and how it compares with other species. The highest priorities for research include development of standardized methods for monitoring populations and

implementation of a regional monitoring program. Given large-scale changes in marine food webs and climate observed in recent decades (Piatt and Anderson 1996, Anderson and Piatt 1999), it seems likely that Horned Puffin populations have undergone fluctuations comparable to those of other seabird species in Alaska. However, we have almost no data with which to assess population trends, and population monitoring is clearly a priority (Byrd et al. 1993). Immediate attention should be focused on the few large colonies that account for most of the total population. To develop monitoring protocols, we need data on colony attendance patterns (diurnal, seasonal, annual, and geographic variability) and factors that influence attendance (weather, food availability, behavior, age-class composition). Studies of marked individuals are essential for interpretation of attendance data. To assess causes of population change, we need more studies in different locations of key population parameters such as productivity, feeding ecology and behavior, and adult survival. Studies should also measure impacts of human activities (e.g., oil pollution, gill-net mortality, harvest, etc.), but in the absence of information on population status, such data would be difficult to interpret and, therefore, of lower priority.

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Appendix 1. Diet of Horned Puffin chicks by colony (arranged from west to east). Data shown as percentage of total prey items observed in meals collected from adults delivering food to young.

Location	Talan I.	Buldir I.		Sozavarika I.	High I.	Midun I.	Shumagin Is.	Suklik I.		Barren Is.	Chisik I.	
Sources[1]	A	B	C	D	E	E	F	D	E	G	H	I
Years collected	1987–1988	1975	1988–1991	1987	1994	1993–1994	1976–1977	1985–1987	1991–1994	1976–1977	1979	1995–1998
Meals sampled	189	15	136	16	22	8	18	580	601	22	199	291
Prey items (n)	1,049	52	800	139	142	28	161	4,596	3,473	77	457	2,030
Fish												
Gadidae	4.8	0.0	5.9	4.3	19.0	28.6	10.6	1.2	13.6	1.3	0.0	0.0
Sand lance	58.7	42.3	64.2	86.3	81.0	32.1	66.5	90.1	63.9	42.9	98.9	94.1
Capelin	5.1	0.0	0.0	2.9	0.0	25.0	21.1	2.3	1.7	51.9	0.7	2.0
Greenling	4.0	0.0	14.6	0.0	0.0	0.0	0.0	2.3	7.1	1.3	0.0	0.0
Other fish	26.8	44.2	2.5	6.5	0.0	14.3	1.8	3.0	9.5	2.6	0.4	3.7
Total fish	99.3	86.5	87.2	100.0	100.0	100.0	100.0	98.9	95.8	100.0	100.0	99.9
Invertebrates												
Squid	0.3	13.5	12.8	0.0	0.0	0.0	0.0	1.1	0.5	0.0	0.0	0.1
Crustacea	0.4	0.0	0.0	0.0	0.0	0.0	0.0	<0.1	3.5	0.0	0.0	0.0
Total invertebrates	0.7	13.5	12.8	0.0	0.0	0.0	0.0	1.1	4.2	0.0	0.0	0.1

[1]Sources: A = Kitaysky 1996; B = Wehle 1983; C = J. Williams and V. Byrd unpubl.; D = Hatch and Sanger 1992; E = J. F. Piatt et al. unpubl.; F = Moe and Day 1979; G = Amaral 1977, Manuwal and Boersma 1977; H = Jones et al. 1980; I = A. Harding and JFP unpubl., Harding 2001.

Appendix 2. Diet of adult Horned Puffins, collected during summer, by location (arranged from north to south). Birds from Central N. Pacific collected year-round, and include sub-adults.

Location	Cape Thompson	Pribilofs		W. Aleutians	Aleutians	Gulf of Alaska		Central N.Pacific
Sources[1]	A	B	C	D	E	F	G	H
Years collected	1959–1961	1975–1978	1984	1975	1988–1998	1969–1978	1988–1998	1990–1992
Stomachs (n)	8	39	15	47	38	40	101	18
Prey items (n)	5	50	?	59	879	?	1,010	118
Percentage measured	Number	Number	Biomass	Number	Biomass	Volume	Biomass	Number
Fish								
Myctophidae	0.0	0.0	0.0		<0.1	0.0	0.0	70.3
Gadidae	30.8	24.0	26.0		50.3	0.8	38.5	0.0
Sand lance	23.0	12.0	0.0		8.8	26.9	40.6	0.0
Capelin	7.7	2.0	0.0		0.0	50.2	0.2	0.0
Other fish	7.7	24.0	26.1		3.3	1.2	0.8	8.5
Total fish	69.2	62.0	52.1	23.7	62.4	87.1	80.0	78.8
Invertebrates								
Squid	0.0	8.0	47.5	67.8	33.4	10.4	19.4	20.3
Polychaetes	15.4	20.0	<0.1	8.5	3.5	0.2	0.6	0.0
Crustaceans	7.7	10.0	0.4		0.8	1.9	0.0	0.0
Other invertebrates	7.7	0.0	<0.1		<0.1	0.4	<0.1	0.9
Total invertebrates	30.8	38.0	47.9	76.3	37.7	12.9	20.0	21.2

[1]Sources: A = Swartz 1966; B = Hunt et al. 1981a; C = Bradstreet 1985; D = Wehle 1982; E = JFP, Springer et al. 1996; F = Sanger 1983; G = JFP; H = P. J. Gould unpubl.

Appendix 3. Measures of Horned Puffin breeding parameters.

Location	Year	Number of nests	% hatching	% fledging	Number of chicks fledged/nest	Source[1]
Barren Is.	1976	14	79	36	0.29	A
	1977	14	93	69	0.64	B
	1978	18	89	81	0.72	C
Chisik I.	1978	25	73	92	0.67	D
	1979	23	44	71	0.31	D
	1993	?	53	69	0.37	E
	1995	21	71	92	0.66	F
	1996	51	84	83	0.70	F
	1997	48	67	96	0.64	F
	1998	61	69	89	0.62	F
	1999	47	77	92	0.70	F
Semidi Is.	1976	42	76	59	0.45	G
	1977	37	68	50	0.34	G
	1979	58	83	83	0.69	H
	1980	56	64	75	0.48	H
	1981	59	85	86	0.73	H
	1983	100	?	?	0.77	H
	1995	32	47	?	?	I
	1998	34	79	?	0.68	I
Ugaiushak I.	1977	68	76	91	0.69	J
Big Koniuji I.	1976	20	80	90	0.72	K
Hall I.	1976	12	83	100	0.83	K
St. Paul I.	1976	25	56	79	0.44	L
	1977	10	90	83	0.75	L
Buldir I.	1988	38	66	32	0.21	M
	1989	39	82	63	0.51	M
	1990	52	77	60	0.46	M
	1991	71	63	62	0.39	M
	1992	24	54	85	0.46	M
	1993	18	89	56	0.50	M
	1994	35	83	62	0.52	M
	1995	38	76	69	0.53	M
	1996	51	75	82	0.61	M
	1997	52	69	83	0.58	M
	1998	39	59	61	0.36	M
Talan I.	1987	27	89	25	0.22	N
	1988	30	77	43	0.33	N
	1989	58	88	90	0.79	N
	1990	40	80	84	0.68	O
	1991	44	77	100	0.77	O
	1992	62	95	59	0.56	O
	1993	62	89	69	0.61	P
	1994	20	?	?	0.60	P
Total average	43	1,675	75.0	73.1	0.562	

[1]Sources: A = Amaral 1977; B = Manuwal and Boersma 1977; C = Byrd et al. 1993; D = Jones et al. 1980; E = Slater et al. 1995; F = A. Harding and JFP unpubl.; G = Petersen 1983; H = Hatch and Hatch 1990; I = Nevins and Adams 1999; J = Wehle 1980; K = Moe and Day 1977; L = Hunt et al. 1981a; M = J. Williams and G. V. Byrd unpubl.; N = Kitaysky 1996; O = Kitaysky 1996, Golubova 1992; P = Kitaysky 1996, E. G. Golubova unpubl.

Appendix 4. Linear measurements (mm) and body mass (g) of adult Horned Puffins. Data shown as mean ± SD (n).

Latitude/longitude	68°N 166°W	63°N 72°W	60°N 167°W	57°N 170°W	59°N 149°E	52°N 176°E	53°N 167°W	55°N 160°W	57°N 156°W
Region	Cape Thompson	St. Lawrence I.	Nunivak I.	Pribilof Is.	Talan I.	W. Aleutian Is.	E. Aleutian Is.	W. Alaska Peninsula	E. Alaska Peninsula
Sources[1]	A	B	B	C	D	E	E	E	E
Bill length									
Male	50.5 ± 2.0 (7)	51.6 ± 2.8 (8)		51.2 ± 4.7 (5)	49.3 ± 2.4 (34)	47.3 ± 0.5 (2)	47.5 ± 2.4 (4)	50.2 ± 2.0 (21)	47.9 ± 2.7 (9)
Female	48.4 ± 2.1 (10)	50.8 ± 2.1 (9)		47.0 ± 3.3(6)	47.5 ± 1.8 (32)	45.0 ± 1.0 (5)	45.1 ± 2.5 (3)	46.8 ± 2.3 (17)	46.4 ± 0.9 (9)
Bill depth									
Male					40.8 ± 3.6 (8)			42.3 ± 2.2 (21)	
Female					40.9 ± 1.9 (9)			40.3 ± 1.7 (17)	
Tarsus									
Male					31.3 ± 1.9 (35)	29.8 ± 2.1 (2)	33.5 ± 3.8 (3)	31.0 ± 1.3 (21)	32.3 (1)
Female					30.2 ± 1.7 (32)	30.4 ± 1.0 (5)	31.7 ± 3.2 (2)	30.4 ± 1.3 (17)	30.7 ± 0.6 (2)
Wing-chord length									
Male	199.6 ± 4.1 (7)	190.2 ± 6.9 (6)[2]		187.5 ± 3.0 (4)[2]	190.2 ± 6.1 (35)	180.5 ± 10.6 (2)	191.8 ± 3.8 (4)	191.6 ± 5.5 (21)	191.4 ± 5.3 (9)
Female	197.0 ± 10.7 (10)	187.4 ± 3.5 (8)		182.3 ± 6.1 (3)	185.7 ± 6.5 (32)	179.6 ± 3.8 (5)	186.0 ± 4.6 (3)	186.2 ± 5.4(17)	188.8 ± 6.5 (9)
Mass									
Male	648.0 ± 24.3 (7)	609.0 ± 54.0 (13)	629.0 ± 54.0 (7)	581.5 ± 32.5 (19)	529.9 ± 48.5 (35)	511.0 ± 34.1 (27)	551.9 ± 43.4 (16)	569.7 ± 45.4 (37)	542.9 ± 47.6 (49)
Female	618.0 ± 47.3 (8)	589.0 ± 47.3 (9)	581.0 ± 48.0 (11)	536.8 ± 41.2 (12)	512.5 ± 49.1 (32)	483.0 ± 31.5 (49)	531.0 ± 46.3 (15)	513.1 ± 40.0 (48)	501.0 ± 41.8 (35)

[1]Sources: A = Swartz 1966; B = Sealy 1973; C = U.S. Fish and Wildlife Service files; D = Kitaysky 1996; E = JFP.
[2]Unflattened wing-chord.

Appendix 5. Linear skeletal measurements (mm) and mass (g) of adult Horned Puffins (J. F. Pitocchelli unpubl.). Data shown as mean ± SD (*n*).

	Males	Females	Significant difference ($p < 0.01$)
Premaxillary length	30.04 ± 1.48 (11)	28.10 ± 1.44 (19)	yes
Bill depth	21.78 ± 1.23 (12)	19.21 ± 1.10 (20)	yes
Interorbital width (maximum)	9.95 ± 0.54 (18)	9.34 ± 0.43 (27)	yes
Interorbital width (minimum)	6.10 ± 0.44 (19)	5.58 ± 0.40 (25)	yes
Skull width	30.72 ± 0.82 (17)	28.97 ± 0.82 (27)	yes
Skull length	80.05 ± 1.59 (15)	76.15 ± 1.72 (20)	yes
Mandible length	62.96 ± 1.76 (19)	60.10 ± 1.82 (23)	yes
Coracoid length	36.98 ± 0.80 (19)	35.89 ± 1.10 (27)	yes
Scapula length	59.30 ± 1.39 (19)	57.99 ± 1.75 (27)	yes
Sternum length	88.45 ± 2.74 (17)	87.27 ± 2.74 (25)	no
Keel length	100.09 ± 3.60 (17)	97.03 ± 2.90 (25)	yes
Keel depth	32.29 ± 1.08 (19)	31.74 ± 1.24 (27)	no
Synsacrum width (maximum)	20.83 ± 1.14 (19)	20.71 ± 0.76 (27)	no
Synsacrum width (minimum)	41.07 ± 1.95 (19)	39.95 ± 1.24 (26)	$p = 0.02$
Tibiotarsus length	65.83 ± 1.88 (19)	62.75 ± 3.32 (27)	yes
Tarsometatarsus length	29.42 ± 0.96 (19)	29.63 ± 6.36 (27)	no
Humerus length	68.76 ± 1.23 (19)	66.89 ± 1.54 (27)	yes
Radius length	54.71 ± 1.28 (19)	53.29 ± 1.23 (27)	yes
Ulna length	55.79 ± 1.28 (19)	54.23 ± 1.29 (27)	yes
Carpometacarpus length	36.00 ± 0.81 (19)	34.79 ± 1.55 (27)	yes
Fresh mass	571.58 ± 40.2 (19)	522.89 ± 39.8 (27)	yes

ABOUT THE AUTHORS

John F. Piatt received his doctorate from Memorial University of Newfoundland in 1987, studying the feeding ecology and population biology of Atlantic Puffins and Common Murres. Since 1987, he has studied seabirds and marine ecosystems in Alaska, with research focused on the pelagic ecology of alcids in the Gulf of Alaska and Bering Sea. He is currently a research scientist with the Biological Resources Division of the U.S. Geological Survey. Current address: Alaska Biological Science Center, USGS, 1011 East Tudor Road, Anchorage AK 99503. E-mail: john_piatt@usgs.gov. Web site: www.absc.usgs.gov/research/seabird&foragefish/index.html.

Alexander (Sasha) S. Kitaysky received his doctorate from the University of California at Irvine in 1996, studying behavioral, physiological, and reproductive responses of puffins and auklets to environmental variability in the Sea of Okhotsk (Russia). Since 1997, he has studied hormonal regulation of parent-offspring interactions of seabirds in Alaska. The main focus of his current research is analysis of evolutionary costs and benefits associated with increased secretion of stress hormones observed in adult seabirds and their chicks during food shortages. He is a Research Assistant Professor at the University of Washington. Current address: Department of Zoology, University of Washington, Seattle WA 98195. E-mail: kitaysky@u.washington.edu.

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