

A HISTORICAL PERSPECTIVE ON THE CITRUS-LIKE SCENT OF THE CRESTED AUKLET

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ABSTRACT: The tangerine-like odor produced by breeding Crested Auklets (*Aethia cristatella*) of both sexes has attracted considerable attention recently as researchers attempt to determine its function. Chicks and one-year-old immatures do not produce the odor. Even though the odor has long been known to the Yu'pik people of St. Lawrence Island, naturalists and ornithologists visiting seabird colonies on the Aleutian Islands and in the Bering Sea from the mid-1700s through first half of the 20th century did not mention the odor. I trace the steps of two early ornithologists, Charles H. Townsend and Ira N. Gabrielson, whose numerous visits to auklet colonies in the late 1800s and 1940s, respectively, provided opportunities to smell the scent. The odor was eventually described on the basis of specimens smelled during preparation and on the basis of encounters with the auklets at sea. The closely related Whiskered Auklet (*A. pygmaea*) also produces an odor, but its function requires study.

The plumage of both males and females of the highly social Crested Auklet (*Aethia cristatella*) exudes an odor like that of a tangerine. The odor is more intense during the breeding season (Douglas et al. 2001, Hagelin et al. 2003). During the stereotyped “ruff-sniff” courtship display (Figure 1), males and females rub their bills in turn in the feathers of the nape and neck of their displaying partners (Jones 1993, Jones and Hunter 1993, Hunter and Jones 1999). How the scent is produced is a mystery, but studies are elucidating its function. Observations and experiments suggest that these chemical signals serve “at least a general social function” (Hagelin et al. 2003, Jones et al. 2004:71) or that the constituents of the odor repel ectoparasites and, therefore, possibly signal a mate's quality (Douglas et al. 2001, 2004, 2005a, b; see Hirth 2005 for a popular account). Although the secrets of this scent are being unlocked now, it was not until the late 1950s that the scent was mentioned in the scientific literature, despite more than a century of exploration of the seabird colonies in the Bering Sea region by naturalists and ornithologists, many of whom must have detected the odor.

This odor aroused my curiosity when I initiated a study of the breeding biology of Parakeet (*A. psittacula*), Least (*A. pusilla*), and Crested auklets in 1966 and 1967 at a mixed colony near the village of Gambell on the Northwest Cape of St. Lawrence Island, in the northern Bering Sea (Sealy 1968). Jean Bédard had been studying ecological segregation among these auklets for two years and was familiar with the odor. We detected it readily at the colony and on the sea, sometimes before we saw the birds, in dense fog and when the wind blew toward us, or when it was calm. Our observations were by no means new, however, because the people of St. Lawrence Island had known about this odor for many generations. In the Yu'pik language, the word for auklets is *sukilpaq* and, with the suffix *-pagni* (“odor of”), *sukilpaqhpagni* becomes “odor of auklets” (David Shinen in litt., 13 April 2004). Elders and others in the village said that the return of Crested Auklets in spring to the waters near their colonies on St. Lawrence Island is heralded by this distinctive odor, which they detected at sea and on calm,

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Figure 1. Crested Auklets engaged in the ruff-sniff display, Kitnik colony near Savoonga, St. Lawrence Island, 2 July 2004.

Photo by Lisa M. Sheffield

overcast days when it wafted through the village. I smelled the scent in the village the first day after my arrival in mid-May in the first year.

AUKLETS IN THE HAND

If the residents of St. Lawrence Island and undoubtedly elsewhere within the range of the Crested Auklet knew about this odor, and because it was so apparent to Bédard and me, it is puzzling that naturalists of long ago did not write anything about it. In *The Birds of Alaska*, Gabrielson and Lincoln (1959) highlighted the history of ornithological exploration in Alaska during the century leading up to the 1950s, and they outlined the itineraries of naturalists who explored the seabird colonies of the Aleutian Islands and Bering Sea region. Georg Wilhelm Steller was the first outsider to record birds in the region, as the naturalist on Vitus Bering's expedition to Alaska in

1741 and 1743–1744. To judge by his extensive travels, especially among the Aleutian Islands and his visits to Bering Island (Stejneger 1936), it is inconceivable that he would not have encountered Crested Auklets, but he mentioned the species only once, when one landed on board the *Elizaveta* during the night of 10 August 1741, on the ship's return to Kamchatka (Stejneger 1936:428). Such landings of Crested Auklets still attract attention (e.g., Dick and Donaldson 1978). Captain James Cook collected the Crested Auklet at "Bird" (St. Matthew) Island on 29 July 1778 (Stresemann 1949), and, beginning with William H. Dall's travels in the Aleutian Islands beginning in the 1870s (see Appendix), through the first half of the 20th century, a succession of naturalists such as Alfred M. Bailey, Arthur Cleveland Bent, Herbert Brandt, Lt. John C. Cantwell, Elliott Coues, Henry Wood Elliott, Ira N. Gabrielson, Joseph Grinnell, G. Dallas Hanna, Francis L. Jaques, E. V. Kozlova, Olaus J. Murie, Edward W. Nelson, Edward A. Preble, Robert Ridgway, Leonhard Stejneger, Charles H. Townsend, and many others (see Gabrielson and Lincoln 1959) visited auklet colonies and wrote extensively about the avifauna of the Bering Sea. None mentioned the Crested Auklet's scent, although surely at least some of them must have detected it. Perhaps they did not associate the scent with birds, especially with one species in particular. This connection would have been difficult to make without birds in the hand, but specimens were collected on those expeditions, and opportunities to smell the odor must have abounded. Notably, the first published description of the odor was based on its detection while specimens of Crested Auklets were being prepared (Humphrey and Phillips 1958). There may have been other reasons.

Naturalists may have detected the odor but did not consider it that remarkable, but this is difficult to imagine. Had they been worried that no one would believe them if they ascribed such a feature to a bird found in such a remote area? Birds emitting odors like this were not well known 100 years ago. Perhaps the odor was not detected because it cannot be smelled every day, and during short visits near and to the colonies the odor might not have been smelled at all. Such failures should not have affected everyone, but before we consider the ability of humans to detect this scent, let us trace the steps of two of these early ornithologists—Charles H. Townsend in the late 1800s and Ira N. Gabrielson in the 1940s—who visited auklet colonies throughout the Bering Sea region, so that we may appreciate the opportunities these individuals would have had to smell this odor.

In a paper devoted primarily to the Crested Auklet, Townsend (1913) described his experiences with this and other species of auklets, first on the Pribilof Islands, where he spent the first three weeks of June 1885 investigating fisheries (see also Townsend 1885, 1927; Mearns and Mearns 1998). During this time, auklets would have been incubating or feeding newly hatched young and the scent should have been prevalent (see Jones 1993), but Townsend either did not detect the odor or he simply never mentioned it. He collected at least one specimen on the Pribilof Islands during this time, and others elsewhere (Appendix), and his detailed descriptions of the plumages of the Crested and other auklets (Townsend 1913) attest that he examined specimens closely. Townsend left the Pribilof Islands on 21 June 1885 on the steamer *Corwin* and arrived 12 days later at the mouth of the

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Kowak River in Kotzebue Sound, having observed Crested Auklets intermittently as the steamer plied its way north (Townsend 1895).

Townsend apparently made four more trips to Alaska, the last in 1895 (Townsend 1897). On each of these trips, he visited several of the Aleutian Islands, but to piece together his itineraries is difficult. On board the *Albatross* in 1888, Townsend traveled from Kodiak Island and the Alaska Peninsula along the entire Aleutian chain toward the Commander Islands off Kamchatka (whether he actually reached this final destination cannot be confirmed, but see Townsend 1913). He did, however, visit several auklet colonies in the eastern and western part of the Aleutian Islands (Townsend 1913, 1927). Townsend's arrival on the Shumagin Islands on 1 August 1888 and his visit to Big ("Koninski") Koniuji Island impressed him. Of the immense numbers of Crested Auklets, he wrote (1913:133), "Rich as our experiences with the Auklets were in many of these places, they did not prepare us for what we were to see in the Shumagin Islands south of the Alaska Peninsula." Flocks of Crested Auklets filled the air, circled over the sea, and lifted off from the colony as he clambered among the boulders, amid which the auklets nested. Although the date was late in the breeding season (see Jones 1993), some scent should have been detectable.

Probably no one visited more seabird colonies than did Gabrielson during his extensive travels in the 1940s (Gabrielson and Lincoln 1959). He visited most of the larger colonies of the Crested Auklet and other seabirds among the Aleutian Islands (Appendix), including Big Koniuji Island, which had been visited by Steller 200 years before (Stejneger 1936), Townsend decades earlier, and where H. D. Douglas III conducted experiments in 2002 (Hirth 2003). Gabrielson also visited colonies on the islands of the Bering Sea, including the Pribilof Islands north to the Diomed Islands (e.g., Gabrielson 1944), which Townsend also had visited decades earlier.

Some of the early naturalists may not have been able to smell the odor. Hector Douglas (in litt., 18 and 19 July 2005) notes that people differ in their thresholds for perception of the Crested Auklet's odor, in nature and in the laboratory. In one laboratory observation, he noted that of five people exposed to the scent of a Crested Auklet specimen, two could not smell the odor at all, whereas three individuals reported the odor was strong. Perhaps some of the early ornithologists had been anosmic, but surely not all of them. We will never know.

DESCRIPTIONS OF THE ODOR

The first published description of the odor produced by Crested Auklets apparently was that of Humphrey and Phillips (1958), based on these authors' separate experiences with auklets early in the 1950s. Philip Humphrey detected the odor quite by accident, inland from the Bering Sea and about 100 km from the nearest breeding colonies. After several days of strong onshore winds in mid-June 1952, Humphrey received four weakened Crested Auklets captured on a freshwater pond at Hooper Bay on the Alaska mainland. While preparing the specimens, he detected (p. 258) "a pungent odor reminiscent of the smell of tangerines" and concluded that the odor "emanated from the region of the bill and was present on all...specimens."

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He commented on the “ornaments” on the bright orange bills, as if implying that the color and the tangerine odor were in some way connected. Humphrey cited Ridgway’s (1919:775) now-confirmed statement that the bill plates are shed at the end of the breeding season and concluded that this odor “stemmed only from the bill ornaments.” Humphrey also noted that museum specimens taken during the breeding season lacked the odor, despite their bills’ remaining brilliant orange.

Early in July 1954, at St. Paul Island, Bering Sea, Richard Phillips noted that two Crested Auklets had “a pleasant odor strongly reminiscent of that of citrus fruits and comparable in strength to a freshly peeled orange” (Humphrey and Phillips 1958:258–259). Days later, Phillips detected the same “pungent” odor at sea and realized that it came from a flock of about 200 Crested Auklets that had flushed about 100 yards ahead of the boat and that the odor disappeared with the birds.

The next observation of the odor was published two years later. In a list of birds observed on Little Diomed Island, Kenyon and Brooks (1960:461) observed “the citrus-like odor of [the Crested Auklet] is often quite noticeable, both on the water and in nesting areas. On May 29 [1958] the odor of a flock of about 10,000 auklets was quite strong at least half a mile downwind while the birds were hidden from view by fog.” These and Phillips’s observations confirmed that Crested Auklets produce this odor at least during the breeding season. The Parakeet Auklet, Least Auklet, and other seabirds were present on St. Paul and Little Diomed islands when some of these observations were made, but the authors associated the odor with the Crested Auklet only.

The odor was mentioned in a study of the functional anatomy of 23 orders of birds (Bang 1971), in two dictionaries of birds (Thomson 1964, Campbell and Lack 1985), and in a survey of birds odorous or unpalatable to humans (Weldon and Rappole 1997). Bang (1971:40) noted that the bill plates had been described as smelling of tangerines during the breeding season, but there were no inferences that olfaction was important to this or any other species of the Charadriiformes, and the Crested Auklet is unremarkable anatomically. Neither Thomson (1964) nor Campbell and Lack (1985) indicated the source of their information, although when describing the structure of the Crested Auklet’s bill, Thomson (1964:67) noted “the plates give out an odour like that of tangerine oranges.” Discussing the scents emitted by several species of birds, scents produced by the uropygial or oil glands, Campbell and Lack (1985:406) noted that the “noticeable odor” of Crested Auklets seems not to be produced by the oil gland.” Weldon and Rappole (1997), citing Thomson (1964), listed among the alcids only the Crested Auklet as one of the species of birds producing an odor.

SOURCE AND FUNCTION OF THE ODOR

Shedding of the bill plates after the breeding season suggests the bill as the source of the scent, but any connection between this molt and the cessation of the production of odor at this time is tenuous, likely coincidental. I definitely detected odor less toward the end of the breeding season, but fewer birds were visiting the colony then, and the intensity of odor would have

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been less. Douglas (pers. comm.) points out that detection of an odor is one thing, but concluding that it no longer is being produced, because it cannot be smelled, is another. But other anecdotal observations suggest that the odor is produced only during the breeding season, and these are supported by recent experimental evidence in favor of a breeding function. Hagelin (pers. comm.) notes that the odor declines noticeably in captive Crested Auklets at the end of the breeding season. Three black-billed second-year Crested Auklets collected at sea on 10 July 1966 were odorless. These individuals lacked brood patches (see Bédard and Sealy 1984), and birds of this age seldom visit the colonies (Jones 1993). I also did not detect the scent among the 15 Crested Auklet chicks I measured daily while quantifying growth, or among eight fledglings captured among the boulders on their way to sea (Sealy 1968). All that is known about the initiation of production of odor prior to breeding is that it is detectable as soon as the birds return in spring to the waters near the colonies.

WHISKERED AUKLETS PRODUCE A SIMILAR ODOR

Many species of birds produce odors that are detectable by humans (Weldon and Rappole 1997), including the Crested Auklet's close relative, the Whiskered Auklet (*A. pygmaea*). Both these auklets produce a citrus-like odor, but their chemical constituents differ (Douglas et al. 2004). Gaston and Jones (1998, see also Jones 1993) alluded to an odor produced by the Whiskered, which is more remarkably ornamented than the Crested, although the bill of the Whiskered is not as brilliantly colored, with little or no orange (Byrd and Williams 1993). On the basis of compatibility analyses of an array of characters of the skeleton, integument, and natural history, Strauch (1985) placed the Whiskered and Crested auklets side by side in his classification of the Alcidae. Focusing on shared characters, Gaston and Jones (1998) hypothesized that the Crested and Whiskered auklets are the most closely related of the true auklets. Friesen et al. (1996) could not discriminate the phylogenetic relationships of these auklets from molecular data, but their findings nevertheless supported Gaston and Jones's hypothesis (1998). In a comparative study of courtship behavior of auklets at sea, Hunter and Jones (1999) observed Crested Auklets performing the ruff-sniff display exclusively and the "neck-twist" display almost exclusively, at sea and on land, whereas Whiskered Auklets performed a display, the "head-bob," at sea (and possibly on land) but did not perform the ruff-sniff or neck-twist displays (Hunter and Jones 1999, Zubakin and Konyukhov 1999, Hagelin in litt., 5 June 2005; Douglas pers. comm.).

Kenyon and Brooks (1960) noted that neither the Parakeet nor Least auklet produces an odor, and Bédard and I never smelled one when either species flew by or flushed at sea or when we handled live or dead individuals, although under these circumstances we smelled the Crested Auklet. It has been determined in the laboratory that the plumages of the Parakeet Auklet (Hagelin et al. 2003) and Least Auklet (Douglas et al. 2004) lack the odor constituents of the Crested Auklet.

UNRESOLVED QUESTIONS

Biologists have only recently begun to appreciate the importance of a sense of smell among birds, having instead focused on song and conspicuous plumage as typical means of communication. Brightly colored bill plates, elaborate forehead crests and auricular plumes, and vocalizations have long been familiar characteristics of the Crested Auklet, but the presence of another sexual "ornament," a chemical signal, possibly adds another dimension to the species' communication system. It also increases the evidence for the importance of smell in birds. Jones (1993:6) noted that for such communication, auklets should respond to one another's odor, and apparently they do (Hagelin et al. 2003). But evidence also exists for chemical defense (Douglas et al. 2004). Experiments now underway should enhance our understanding of this and other signals in the Crested Auklet, and they may be found to act in tandem. Experiments need to be conducted on the Whiskered Auklet. Other questions remain.

What is the selective pressure for the evolution of scent in these auklets? Does the odor vary in intensity or quality from individual to individual, as do the plumage ornaments (Jones 1990, Jones et al. 2000)? Variation would give females a basis for choosing their mates, with the scent functioning as an indicator of the male's quality, as Jones (1993) speculated. Individuals studied over many years may reveal fitness benefits of the odor and reveal costs associated with producing and using it. Jones (1993) wondered whether the scent might be important in social communication among individuals at sea. The scent is especially strong at sea, but possibly it is more detectable there, at least by humans. Why do only two species of auklets produce the odor, and not others with similar ecology and behavior? For so long the odor of the Crested Auklet went unnoticed or undescribed, but its nature and function are finally emerging.

ACKNOWLEDGMENTS

The impetus for this summary of early reports of the Crested Auklet's odor arose from the exciting research of Hector D. Douglas III and Julie C. Hagelin, Ian L. Jones, and collaborators, and my memories of the scent smelled long ago while studying auklets. Many residents of Gambell shared their knowledge of the odor and assisted with my field work in different ways. I am especially indebted to my colleague, Jean Bédard, for sharing his experience and knowledge of alcids, and of St. Lawrence Island. Hector D. Douglas III, Robert H. Day, Julie C. Hagelin, David C. Shinen, Gus B. van Vliet, and Kevin Winker responded to my inquiries for information, and Victor A. Zubakin searched Russian literature for information on the odor. Daniel D. Gibson helped with literature pertaining to C. H. Townsend's travels in Alaska, provided information on place names, and edited the manuscript. Day, Douglas, and Hagelin commented on various drafts of the manuscript, and the latter two generously allowed me to include their unpublished observations. James Dean, United States National Museum, provided information on specimens of Crested Auklets taken by some of the early naturalists (summarized in the Appendix). Peter Capainolo and Maureen Flannery checked the holdings of the Crested Auklet in the American Museum of Natural History and California Academy of Sciences, respectively. I am indebted to Lisa M. Sheffield for inviting me to St. Lawrence Island in 2003 and 2004 where, with Ian C. Rose and Zubakin,

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we enjoyed many discussions about auklets. Sheffield and Ian L. Jones (see inside back cover of this issue) provided the photographs of the Crested Auklets in the ruff-sniff display.

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- Appendix 1. Crested Auklets collected by three early naturalists in Alaska and Russia.
- William H. Dall*.—Five skins are catalogued in the United States National Museum (USNM): USNM 68391 and 68392, July 1874, Big Koniui Island (Shumagin Islands); USNM 61623, 13 December 1871, Unalaska Island; and USNM 65493 (nestling), 3 July 1873, Kyoka (= Kiska) Harbor, Kiska Island. The fifth specimen (USNM 45665) was collected at Plover Bay, Russia, 15 September 1866. There are also several partial skeletons (mostly skulls) from Alaska.

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Charles H. Townsend.—At least four skins and one skeleton: USNM 106870, 8 June 1885, Otter Island (Pribilof Islands); USNM 200969, 19 June (year?), Yukon Harbor (Big ["Koninsky"] Koniuji Island); and USNM 18442 (skeleton), 26 August 1888, Yukon Harbor (Big Koniuji Island). Ridgway (1983) referred to two (more) skins (probably USNM 115847 and 115848) taken on Big ["Koninski"] Koniuji Island on 4 August 1888, during the cruise of the *Albatross*. USNM 115848 was later exchanged with the Albany Museum in South Africa in 1897 (J. Dean in litt., 22 March 2006).

Ira N. Gabrielson.—Sixteen skins in USNM, three from Chagulak Island, one from St. Paul (Pribilof Islands), and 12 from Kasatochi Island.

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White-tailed Ptarmigan (*Lagopus leucura*) along trail to Mt. Audubon, Roosevelt National Forest, Colorado, 24 September 2006, during a field trip from WFO's 31st annual meeting in Boulder, Colorado.

Photo by David Krueper