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Behavior of Crested Auklets (*Aethia cristatella*, Charadriiformes, Alcidae) in the Breeding Season: Visual and Acoustic Displays

V. A. Zubakin[a, b], I. A. Volodin[c, d], A. V. Klenova[c], E. V. Zubakina[b], E. V. Volodina[d], and E. N. Lapshina[c]

[a] *Severtsov Institute of Ecology and Evolution, Russian Academy of Sciences, Moscow, 119071 Russia; e-mail: vzubakin@yandex.ru*

[b] *Russian Bird Conservation Union, Moscow, 111123 Russia*

[c] *Biological Faculty, Moscow State University, Moscow, 119991 Russia*

[d] *Moscow Zoo, Moscow, 123242 Russia*

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Abstract—The crested auklet, a highly social planktivorous bird species of the Northern Pacific, is an important component of marine ecosystems. Although visual and acoustic modalities play a major role in the communication of these birds, the available data on the repertoire of their vocal signals and postures are scarce and lack quantitative analysis. This study deals with visual and acoustic displays of crested auklets on their breeding grounds and the occurrence frequencies of certain forms of social behavior in male and female birds. The data were collected on Talan Island (the Sea of Okhotsk) in 1987–1991 and 2008. They show that the rate of contacts between birds is very high and sex-specific: on average, males initiate 1.13 contacts/min, compared to 0.65 contacts/min initiated by females. Directionality of ruff-sniff displays differs depending on the posture of the recipient bird. The duration of the trumpeting display in males depends on their social surroundings. However, the duration of either the trumpeting display or the mutual cackling display during courtship is independent of the behavioral context. Vocalization of crested auklets is characterized by two independent basic frequencies occurring either sequentially or simultaneously. The role of different communicative modalities in the behavior of the crested auklet is discussed.

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INTRODUCTION

The crested auklet is a planktivorous colonial seabird of the Northern Pacific. The nesting range of this species extends over the coasts and numerous islands of the Bering Sea and the Sea of Okhotsk (Konyukhov, 1990; Jones, 1993; Andreev et al., 2006). The total species abundance is no less than 6×10^6 breeding birds (Jones, 1993; Andreev et al., 2006). In the nesting season, crested auklets occupy sea-facing talus slopes, making their nests at several levels, either close to the talus surface or at a depth of down to several meters. The nesting density is very high: several nests may be located under the same stone. The distance between neighboring incubating birds is sometimes only a few tens of centimeters, but the birds of different pairs are probably not in visual contact with each other in such cases (Zubakin, 1990).

In the breeding season, either before egg laying or during incubation, crested auklets are characterized by a high level of social activity (Zubakin, 1990, 2007; Konyukhov, 1990; Kharitonov, 2007). These birds spend much of time on the surface of rocks or big stones, communicating with conspecific individuals. The social structure of crested auklet colonies is very complex, since the birds maintain long-term social contacts not only with their breeding partners but also with other birds of the opposite sex. A characteristic feature of the crested auklet is the formation of "clubs," assemblages of unmated and nonincubating birds actively interacting with each other. Breeding males may develop a system of dominant–subordinate relationships, which manifests itself in differences in access to preferred display grounds (Zubakin, 1990, 2007; Kharitonov, 2007). Most of social displays are accompanied by various vocal signals (Kharitonov, 1980; Jones, 1993).

During social interactions, crested auklets widely use olfactory communication. Its use in intraspecific interactions is uncommon for birds and has been confirmed only in a few species of Procellarii form birds (Bonadonna et al., 2003, 2007; Bonadonna and Nevitt, 2004; Jouventin et al, 2007) as well as in the crested auklet (Hagelin, 2007; Hagelin and Jones, 2007; Rajchard, 2007). In the beginning of breeding period, adult male and female crested auklets acquire a specific citrus-like scent, which disappears by the onset of autumn molt. Characteristic of the crested auklet is the so-called ruff-sniff display, in which the bird places its bill within the nape feathers of the display partner (Jones, 1993; Hagelin et al., 2003; Zubakin, 2007; Hagelin, 2007). As shown in experiments, crested

auklets can distinguish between conspecific and heterospecific odors (Hagelin et al., 2003; Douglas, 2008) and, when presented realistic life-sized models of conspecific birds, show preference for male models with added odor, compared to the control models (Jones et al., 2004).

Thus, the communicative behavior of crested auklets is highly composite and involves complex visual, acoustic, and olfactory displays. Oddly enough, it is the olfactory communication of this species that has been studied in most detail (Douglas et al., 2001, 2004; Hagelin et al., 2003; Douglas, 2006, 2008; Hagelin, 2007; Hagelin and Jones, 2007). Visual displays are described only in a few general reviews (Kharitonov, 1980; Konyukhov, 1990; Jones, 1993). In two such publications, spectral patterns and short descriptions of some acoustic signals of the crested auklet are presented (Jones, 1993; Seneviratne et al., 2009). The absence of detailed descriptions of visual displays and vocal signals interferes with comprehensive complex analysis of the communicative behavior of this species and its comparison with close alcid species. The purpose of this study was to give a detailed description of visual and acoustic displays of crested auklets in the breeding season.

MATERIALS AND METHODS

The material was collected on Talan Island, in Taui Bay of the Sea of Okhotsk (Magadan Region; 59°18′ N, 149°05′ E), from mid-May to the end of July (1987–1991, 2008). Additional observations were made by V.A. Zubakin on islands in the Bering Sea: Buldyr (1993), Little Diomede (1999), and St. Lawrence (2000–2004). The nest colony of crested auklets on Talan Island in the 1980s consisted of about one million birds (Kondrat'ev et al., 1992), but its size decreased by 2008 to approximately 260–300 thousand birds (Andreev et al., 2009).

Observations on the behavior of crested auklets and audio records of their vocalization in the breeding season were made in the test plot located on the western side of the island, 15 m above sea level, which consisted of taluses, partly bare and partly covered with vesetation. The area of the plot used in 1988 to 1991 was about 190 m^2. In 2008, it was reduced to 82 m^2 (including 40 m^2 of bare rocks), since the birds decreased in numbers and ceased to nest in the greater part of the overgrown talus. The birds were trapped with noose carpets on the surface (on stones) or with nets covering the entrances of nest chambers and banded with an individual set of colored rings and an aluminum ring of the M series (steel rings of the PS series were also used in 2008). Thus, 180 birds were banded from 1988 to 1991, and 75 birds, in 2008. Immediately after trapping, all birds were weighted with a Pesola spring balance to an accuracy of 1 g, and the culmen and bill depth were measured to determine bird sex (Jones, 1993a, 1993b; Jones et al., 2000). The sex of the birds trapped in 2008 was also determined by PCR amplification of DNA from feather samples. To this end, four to five feathers from the breast and belly plumage were taken from each bird. PCR analysis was performed with the P2 and P8 primers specific for the sex chromosomes of birds (Griffiths et al., 1998; Cerit and Avanus, 2007).

Observations with binoculars were made from the blind located 15 m from the center of the plot, during the morning and evening peaks of activity of crested auklets on land (Zubakin and Zubakina, 1992). We used the method of observations on focal birds (Altmann, 1974), keeping records on the behavior of not only the focal bird but also of its nearest social environment, i.e., all other birds within a radius of 1 m. Observations on the social activity of individually banded crested auklets at the onset of the breeding season were performed in May to June 1990. The period of continuous observation of a focal bird was 5 min; comments were recorded with a voice recorder and processed at 2.5-s intervals. On the whole, 1528 min of observations on 24 male and 22 female crested auklets were recorded, with the duration of records dealing with an individual bird varying from 5 to 58 min. We also made records of individual forms of behavior and situation in which they took place, measuring their duration with a stopwatch to an accuracy of 0.2 s.

Crested auklet vocalizations were recorded in 1990, using a Reporter-5P tape recorder with an MKE-100 condenser microphone or MD-80 dynamic microphone, and in 2008, using a Marantz PMD-660 digital audio recorder with an AKG-C1000S electret condenser cardioid microphone. This equipment allowed high-quality sound recording within a frequency range of 50 to 14 000 Hz. The MD-80 and AKG-C1000S microphones were installed 10 cm above the ground surface in the center of the plot, where the birds were most active, so that the distance between the birds and the microphone in the course of recording was no more than 2 m. The MKE-100 microphone was in the blind for observers, and the distance to the birds was 10–15 m. The total duration of records made in 1990 and 2008 was about 40 h.

Using the Avisoft SASLab Pro 4.3 program, bird calls were digitized with 16-bit resolution at a sampling frequency of 22.05 kHz, which was subsequently reduced to 11.025 kHz. The frequency and time parameters of the calls were measured in the spectrogram window using cross-shaped and standard cursors. Spectrograms were plotted using a Hanning window at 1024-point fast Fourier transform (FFT) size, 25% frame, and 98.43% overlap. These settings provided 10-Hz resolution in frequency and 1.45-ms resolution in time. All measurements were automatically recorded in the Excel spreadsheet. A total of 852 calls were analyzed.

Statistical data processing was performed using nonparametric bilateral tests such as Kruskal–Wallis one-way ANOVA, Mann–Whitney test, Spearman

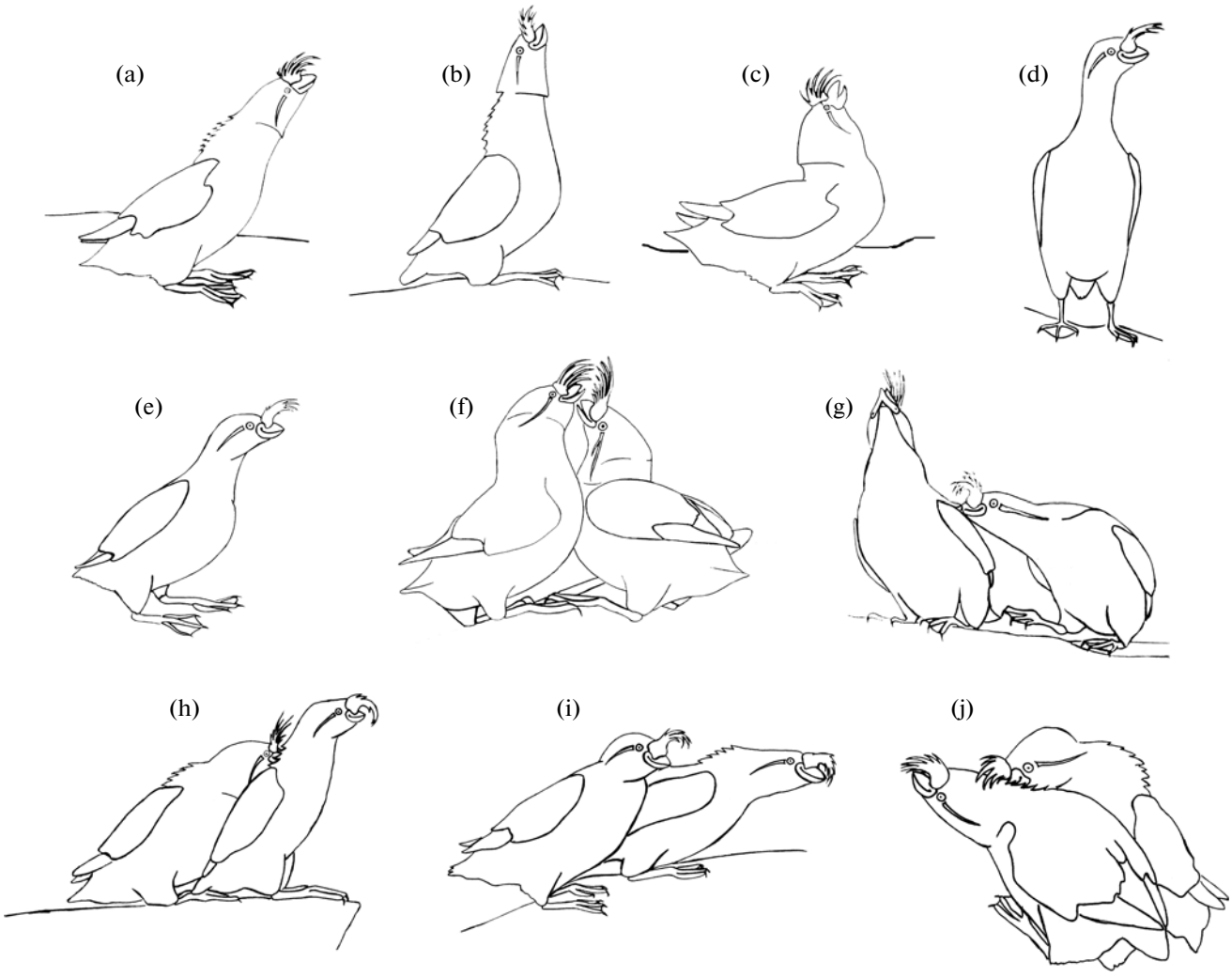

Fig. 1. Postures and visual displays of crested auklets on the scree surface: (a) oblique threat posture, (b) upright threat posture, (c) trumpeting display, (d) alert posture, (e) arch display, (f) billing, (g) touch display, (h, j) riff-sniff displays, and (i) oblique posture with throat presentation.

rank correlation test, and White test (Statistica 6.0 program package). Differences were considered significant at $p < 0.05$. The results were presented as mean values with standard deviations ($x \pm SD$).

RESULTS

Postures and Visual Displays

Crested auklets use several threat postures. A bird in the ***oblique threat posture*** (Fig. 1a) has its neck stretched obliquely forward or forward and up, with feathers on the neck, nape, and cheeks ruffled up. The head is raised in line with the neck, the crest overhanging the bill. The body is often also in line with the neck, its anterior part being raised, but it can as well be pressed to the ground or even slightly raised posteriorly. The bird in this posture periodically thrusts its bill toward an adversary (directly, or above, or at an angle when sitting sideways to it) and can well peck another auklet. Otherwise, this posture is often assumed after pecking the adversary.

An alternative variant is the ***upright threat posture*** (Fig. 1b) with the neck and bill extended straight up and feathers on the neck and cheeks ruffled. The bird periodically stretches out the neck, thrusting the bill upward, and shakes its head (probably, to clear nasal ducts from mucus and salt gland secretion). The upright threat posture is similar to the trumpeting display posture (see below) and sometimes indeed changes into the latter. Kharitonov (1980) named it a "predisplay posture."

Another alternative is the ***crouched threat posture*** where feathers on the neck are ruffled but the neck itself is drawn in, with the shoulders hunched up. The bill points forward, with the crest projecting above it. This posture is less frequent than the oblique and upright threat postures but most often results in an attack on the adversary.

During aggressive interactions, crested auklets try to oust each other while being in a threat posture. These displays (especially in the crouched and upright postures) often result in open fight. However, despite being obviously aggressive, threat displays (oblique and upright in particular) attract females and nonaggressive males, which make attempts to put their bills into the back or nape plumage of the displaying bird (see below).

Males use threat postures more often, but females also display them during interactions with other birds, either male or female. In some pairs, a reversal of behavior was noted (Zubakin, 1990): the female (rather than the male) ruffled feathers on the head and neck, assumed threat postures, and attacked all neighboring auklets, while the male remained in the posture characteristic of arch display (see below), with smooth plumage, and behaved peacefully.

A bird in the ***alert posture*** (Fig. 1d) stands on toes or sits leaning on tarsometatarsi with the body stretched upright and the neck raised up and slightly bent forward. The plumage is kept smooth, and the bird looks lean and thin-necked. The bill points forward. This posture is typical for both male and female crested auklets when they are alarmed by an approaching predator or a human or by a sudden take-off of other birds.

A less strained variant of this posture, with the neck raised to a lesser extent, is known as the "arch display" (Jones, 1993) (Fig. 1e). It is characteristic of females during contacts with males that are in a threat posture. Arch displays are also used by males to reduce the probability of attacks from courting and aggressive males (Zubakin, 1990, 2007).

During the ***trumpeting display*** (Jones, 1993), or courtship display (Kharitonov, 1980) (Fig. 1c), the bird perks its head up so that the neck, bill, and crest are in a straight line. The chest is puffed out, and the plumage on the neck and cheeks is ruffled so that the neck looks thick and the head "high-cheekboned," almost triangular. The white stripes of ornamental head feathers are not appressed but extend to the sides. The trumpeting display was observed almost exclusively in males, females used it very rarely (1.08% of cases, $n = 186$). It is usually accompanied by a specific vocalization named trumpeting call (see below). When the bird is making this call, its neck and chest puff in and out in time with sounds, and the tail slightly moves up and down. The trumpeting posture together with the trumpeting call are a self-advertisement display repeated by males throughout the breeding season, both near the nests and on stones covering the colony area. This is the most typical element of male "club activity" (Zubakin, 1990, 2007). As the threat postures, the trumpeting display attracts other auklets, which attempt to place their bills into the nape or back plumage of the displaying bird or at least touch it.

The duration of male trumpeting display varied from 2.0 to 8.8 s, averaging 4.3 ± 1.3 s ($n = 184$) and depended on the male social environment within a radius of 1 m. If the billing partner (see below) was near, this duration (3.4 ± 0.9 s, $n = 18$) was shorter than in the presence of other auklets (4.5 ± 1.5 s, $n = 66$) or in their absence (4.3 ± 1.1 s, $n = 100$) (Mann–Whitney test, $U = 323$, $p < 0.01$ and $U = 434$, $p < 0.001$, respectively). However, the duration of the trumpeting display in different situations proved to be almost the same: 4.1 ± 1.0 s ($n = 41$) near the nest, 4.1 ± 1.4 s ($n = 57$) in an aggressive situation, and 4.5 ± 1.2 s ($n = 50$) during male vocal duels(Kruskal–Wallis ANOVA, $H = 5.7$, $p = 0.06$).

Billing, or pair courtship (Kharitonov, 1980), or courtship with mutual cackling vocal display (Jones, 1993) is a typical pair display in the crested auklet (Fig. 1f). The birds sit closely opposite each other, with their bills brought together (often in contact) and the necks looking thick because of ruffled plumage, and gently "pinch" at the partner's bill and feathers on the chin and cheeks at the bill base.

Billing is an essential component of pair formation in crested auklets. This display usually becomes more harmonious when the male and female partners become well acquainted with each other. Sometimes, especially at the beginning of breeding season, we observed billing partners behaving aggressively, with touches to the partner's plumage changing into pecks. Probably, these pairs were not yet formed completely. Billing was often noted at the moment of partners' meeting, e.g., when the birds replaced each other on the nest. In addition, both males and females demonstrate extra-pair billing with "club" partners, sometimes with several birds in a series (Zubakin, 1990; 2007). In most cases two birds of opposite sexes are involved in billing. Occasionally, we observed a male joining the pair in billing. In one case, such a male ousted the female and completed the display with the male partner.

Billing was usually accompanied by vocalization (cackling) of both partners (see below), but 15.4% of billing displays were silent ($n = 214$). Silent displays took place mainly when there were no other birds within a radius of 1 m (55.6% of cases, $n = 18$), whereas billing with cackling was usually observed in the presence of other crested auklets (92.2%, $n = 77$). This is evidence that billing with cackling not only contributes to consolidation of the pair but also serves as an aggressive display against neighboring birds.

The duration of billing displays with cackling varied from 3.8 to 13.8 s, averaging 6.5 ± 1.8 s ($n = 88$), whereas that of silent display was significantly longer, 8.3 ± 5.2 s ($n = 17$) (Mann-Whitney test, $U = 20$, $p < 0.001$). The duration of displays with cackling in different situations was the same (Kruskal-Wallis ANOVA, $H = 3.2$, $p = 0.36$): 5.9 ± 1.2 s ($n = 6$) when billing partners met, 6.6 ± 1.8 s ($n = 66$) during disturbances near the nest, 6.7 ± 2.1 s ($n = 20$) upon stimulation by the partner, and 7.7 ± 2.6 s ($n = 11$) in an aggressive situation.

Tactile contacts involving the use of the bill play an important role in auklet communication and are widely used in displays of breeding partners, but their functional significance is as yet unclear (Zubakin, 2007). Evidence for the importance of tactile contacts in the mating behavior of crested auklets (which mate in the sea) comes from the fact that mating usually takes place only after the female swimming next to the male touches his nape plumage with her bill (observations by V.A. Zubakin). Two types of such tactile contacts are distinguished, with the boundary between them being fairly arbitrary. These are ***touch display*** and ***ruff-sniff display***.

Touch display (Jones, 1993) is when birds carefully touch their bills to feathers on the throat, bill base, nape, or back of the bird performing a display of a different type (Fig. 1g). This occur primarily during threat (oblique or upright), trumpeting, or billing displays.

The displaying auklet can oust the other bird but often pays no attention to its touch. In the absence of obvious aggression, the touch can develop into more intensive interaction named the ***ruff-sniff display*** (Jones, 1993) (Fig. 1h). In this case, the birds can fully insert their half-open, quivering bills into each other's plumage.

The displaying bird or a pair of birds often attracts the attention of many neighboring birds (both males and females), which make attempts to approach and place their bills into the plumage of this bird as deep as possible. They try to touch the displaying birds on the head but approach them from behind (to avoid pecks) and, hence, have access only to the nape and back plumage.

If the neighbors are many, some of them cannot approach the displaying bird(s) and address ruff-sniff displays to the birds in front of them. As a result, the group of birds is sometimes transformed for a few seconds into a cluster of entangled bodies. If the displaying auklet starts to move, other birds follow it in lines of two to four individuals, each with the bill placed into the plumage of the preceding bird (Zubakin, 2007).

The touch and ruff-sniff displays of crested auklets play an important role in the process of pair formation. At the beginning of the breeding season, crested auklets often respond to touch by the display referred to as **oblique posture with throot presentation** ("neck-twisting" by Jones, 1993) (Fig. 1i) The bird holds it neck parallel or at a slight upward angle to the ground and slightly bent, with its plumage ruffled (especially on the dorsal surface), and walks alongside its partner, periodically twisting the neck so that its ventral part is exposed to the other bird. This is usually a male display, but it can also by observed in females or in both members of the pair. Neck twisting often leads to close contact followed by the ruff-sniff display (Fig. 1j). At the beginning of pair formation, tough displays may have a form of pecks and pulls at the partner's plumage.

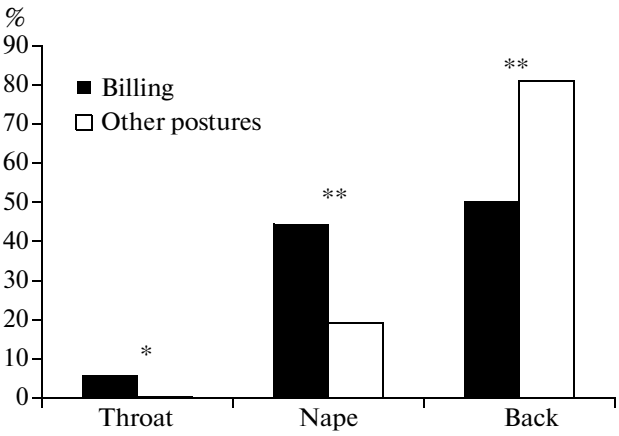

Fig. 2. Dependence of the zone of bill placement during ruff-sniff displays (throat, nape, or back) on the posture of recipient bird. Solid bars refer to the billing posture; clear bars, to postures during trumpeting and oblique or upright threat displays or at rest. None of the recipient birds was a breeding or "club" partner of the displaying bird. Differences are significant at $*p < 0.01$ or $**p < 0.001$ (White test).

Neck twisting may be accompanied by babbling (see below).

The functions of ruff-sniff displays are unknown. The hypothesis that they serve to reduce aggressiveness of the recipient bird has proved erroneous (Zubakin, 2007). Conversely, the recipient often attacked the displaying bird, evoking the aggressive response. Apparently, neighboring birds are attracted by the citrus-like scent characteristic of crested auklets in the first half of the breeding season (Hagelin et al., 2003; Jones et al., 2004; Hagelin, 2007; Douglas, 2008).

We analyzed how the zone of bill placement during ruff-sniff displays (throat, nape, or back) depended on different factors. No dependence was revealed for factors such as season (spring before egg laying vs. summer during incubation) (Kruskal–Wallis ANOVA; $H = 0.03, p = 0.86$), the sex of the displaying bird ($H = 0.4, p = 0.53$), or the sex of the recipient bird ($H = 0.2, p = 0.66$) have not been revealed. Only the posture of the recipient bird proved to have a significant effect on the zone of bill placement (Kruskal–Wallis ANOVA; $H = 45.4, p < 0.001$). When the recipient bird was one of a billing pair ($n = 214$ records), displaying birds attempted to place the bill into feathers on its nape, neck, or (less frequently) throat (Fig. 2). If the recipient bird was in the trumpeting or threat posture (oblique or upright) or at rest ($n = 196$ records), the displaying birds usually examined feathers on its back or, less frequently, nape, almost never touching the throat (all differences are significant according to the White test) (Fig. 2).

We also revealed sex-dependent differences in the direction of ruff-sniff displays in pairs of breeding or club partners (Fig. 3). Males ($n = 100$ records) more often placed their bills into feathers on the nape of a

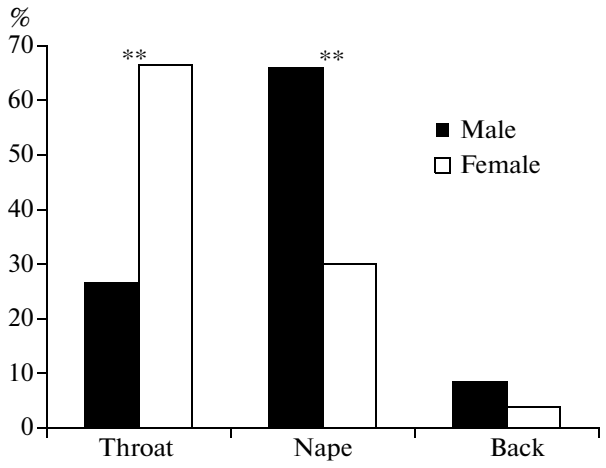

Fig. 3. Sex-dependence differences in the direction of bill placement during ruff-sniff displays (throat, nape, or back) in pairs of breeding or "club" partners. Solid and clear bars refer to males placing the bill into the plumage of a female partner, and vice versa, respectively. Differences are significant at $^{**}p < 0.001$ (White test).

female partner; females ($n = 80$ records), on the throat of a male partner (White test, $p < 0.001$ in both cases). Feathers on the back were less attractive for either male or female displaying birds.

Sounds and Acoustic Displays

Vocalizations of crested auklets were characterized by two basic frequencies, one in the range of 0.35–0.80 kHz, and the other, 0.96–1.15 kHz (table). The low and high basic frequencies occurred either independently, in separate sounds, or in one sound. In the latter case, either a drop from high to low frequency or biphonation were recorded (Wilden et al., 1998; Volodin et al., 2005; Zollinger et al., 2008). Low-range frequency jumps within one sound also took place. However, high- and low-range frequencies within the same sound never overlapped with each other.

Separate calls in the crested auklet are relatively rare; they are usually combined into sequences of structurally similar or different sounds. We distinguished five structural classes of calls in this species.

Babbling (Figs. 4a–4d, table). This term refers to short, low sounds differing in frequency modulation profile and often emitted in series, at irregular intervals. On the whole, 250 records of babbling were analyzed. Among them, only the low basic frequency was found in 52.4% of cases (Fig. 4a); only the high basic frequency, in 8.4% of cases (Fig. 4d); both basic frequencies occurring either sequentially or simultaneously (Fig. 4d) were recorded in 39.2% of cases. Both males and females usually babbled in relatively quiet situations, while not interacting with other birds. Babbling sounds were also often emitted by partners in billing, during intervals between low-intensity cackling (especially short cackling without the main part); in addition, some males included them in the trumpeting call (see below).

Barks (Jones, 1993; Seneviratne et al., 2009) are short, loud calls with an arc-shaped frequency modulation profile that are emitted either singly or in series, at irregular intervals (Fig. 4f, table). Barks, recorded both in males and females, were usually characterized by the low basic frequency, with the high frequency occurring in only 3.1% of cases ($n = 225$). Their distinctive feature are low-range frequency jumps, one or two per call. Barks were usually emitted by birds in the state of anxiety, in case of alarm or danger, and also during flight.

Serial barks, which probably correspond to "hooting" (Jones, 1993), are the sequences of calls structurally analogous to barks but emitted at relatively regular intervals of 236 ± 80 ms (Fig. 4g, table). The duration of a serial bark varied from 2.98 to 16.96 s, averaging 7.44 ± 3.44 s. The number of barks in a series varied from 7 to 48, averaging 17.6 ± 9.42 ($n = 30$). High-frequency sounds could sometimes be revealed between low-frequency barks (in less than 10% of serial barks). Compared to single barks, individual calls in serial bark sequences were significantly longer (Mann–Whitney test, $U = 1169$, $p < 0.001$) and had a lower maximum basic frequency ($U = 623$, $p < 0.001$) (table).

Serial barks were almost exclusively male calls that often interchanged with trumpeting calls. It may well be that their function is also self-advertisement, as is the case with trumpeting calls.

Trumpeting call, also referred to as courtship song (Zubakin, 2007) or simply trumpet (Seneviratne et al., 2009), is the vocal sequence following a strict structural pattern that is performed by crested auklets during trumpeting displays (Fig. 4h, table). The trumpeting call consists of introduction and basic part. The sounds of introduction strongly differ in duration and frequency modulation profile, while the sounds of the basic part are much more stereotyped. The basic part was sometimes followed by several short and low sounds structurally similar to babbling. The introduction consisted of two to four high-frequency sounds (two in 42.3%, three in 57.7%, and four in 3.1% of the calls recorded, $n = 97$). The basic part consisted of two to seven low-frequency sounds (two sounds in 16.5%, three in 36.1%, four in 28.9%, five in 14.4%, six in 3.1%, and seven in 1% of the calls, $n = 97$). In the basic part, low-frequency sounds in the basic part alternated with one to four high-frequency sounds (one high-frequency sound in 47.4%, two in 42.3%, three in 9.3%, and four in 1% of the calls, $n = 97$). Low-frequency sounds in the basic part generally prevailed over low-frequency sounds and did not alternate with them at the end of this sequence. Moreover, only the low-frequency sounds of the trumpeting call could be heard from a distance, because their volume markedly exceeded that of high-frequency sounds.

Measured parameters of individual sounds and sound sequences in vocalizations of crested auklets, $x \pm SD$

Sound type	Low-frequency sounds			High-frequency sounds		
	Sound duration, s	Basic frequency, kHz		Sound duration, s	Basic frequency, kHz	
		Maximum	Minimum		Maximum	Minimum
Low-frequency babbling, $n = 75$	0.07 ± 0.02	0.49 ± 0.07	0.36 ± 0.05	–	–	–
High-frequency babbling, $n = 12$	–	–	–	0.05 ± 0.02	1.26 ± 0.14	1.13 ± 0.16
Biphonic babbling, $n = 63$	0.04 ± 0.01	0.50 ± 0.07	0.39 ± 0.05	0.05 ± 0.02	1.35 ± 0.09	1.14 ± 0.10
Barks, $n = 225$	0.16 ± 0.03	0.79 ± 0.04	0.42 ± 0.09	–	–	–
Serial barks, $n = 30$	0.20 ± 0.03	0.72 ± 0.04	0.40 ± 0.05	–	–	–
Trumpeting call (introduction, last sound), $n = 97$	–	–	–	0.15 ± 0.04	1.24 ± 0.12	0.96 ± 0.13
Trumpeting call (introduction, penultimate sound), $n = 97$	–	–	–	0.56 ± 0.2	1.23 ± 0.34	0.96 ± 0.25
Trumpeting call (basic part), $n = 97$	0.27 ± 0.05	0.70 ± 0.02	0.46 ± 0.06	0.10 ± 0.03	1.22 ± 0.18	0.98 ± 0.13
Cackling (introduction), $n = 119$	0.08 ± 0.01	0.76 ± 0.07	0.44 ± 0.09	–	–	–
Cackling (basic part, first sound), $n = 80$	0.23 ± 0.04*	0.76 ± 0.06*	0.46 ± 0.08*	–	–	–
Cackling (basic part, second sound), $n = 80$	–	–	–	0.10 ± 0.04	1.17 ± 0.10	0.99 ± 0.08
Cackling (basic part, third sound), $n = 80$	0.08 ± 0.02	0.73 ± 0.06	0.47 ± 0.09	–	–	–

The low-frequency sounds in the basic part of the trumpeting call, being structurally similar to single barks, are significantly longer (Mann–Whitney test; $U = 193$, $p < 0.001$), and their maximum and minimum basic frequencies are significantly lower ($U = 934$, $p < 0.001$ and $U = 6932$, $p < 0.001$, respectively) (table). The total duration of the trumpeting call averaged 2.17 ± 0.44 s; the duration of the introduction, 0.89 ± 0.23 s; and the duration of the basic part, 1.28 ± 0.41 s ($n = 97$).

The trumpeting call during trumpeting displays is observed almost exclusively in male crested auklets. Its function is self-advertisement aimed at deterring potential male competitors and attracting females.

Cackling (Jones, 1993) is a complex vocal sequence performed by a male–female pair during billing (Figs. 5a–5g, table). Cackling of one bird without acoustic support of the other is a very rare phenomenon. The complete cackling sequence has three components: introduction and the basic and final parts (Fig. 5a).

Introduction consisted of a sequence of sounds similar to babbling. It often started with high-frequency calls, which were followed by low-frequency calls. The rate of their performance gradually increased from the beginning to the end of introduction. As a rule, one bird started calling, and the other one joined later; during simultaneous vocalization, their calls alternated with each other (Fig. 5b). The basic part was a stereotyped repetition of syllables consisting of three structurally different sounds: each syllable started from a long low-frequency sound, which was followed by a short high-frequency sound and then by a short low-frequency sound (Fig. 5c). The frequency modulation profile of the first sound in the syllable varied from very low to wavelike. When the birds were strongly excited, these calls by the end of the basic part sometimes separated into a rapid series of individual pulses with a bell-shaped frequency modulation profile. The final part, similar to introduction, consisted of a sequence of sounds similar to babbling, with their volume and rate of performance decreasing gradually (Fig. 5d).

In every third case (34%, $n = 250$), auklets failed to complete the cackling sequence and performed only the introduction (Fig. 5g). Each of partners in billing could emit its own sequence of cackling sounds, independently from the other. Hence, in 44.4% of cases ($n = 250$) one birds could already perform the basic or even final part, while the other bird continued to emit introduction calls (Fig. 5e). Both birds performed the basic part of the cackling sequence simultaneously

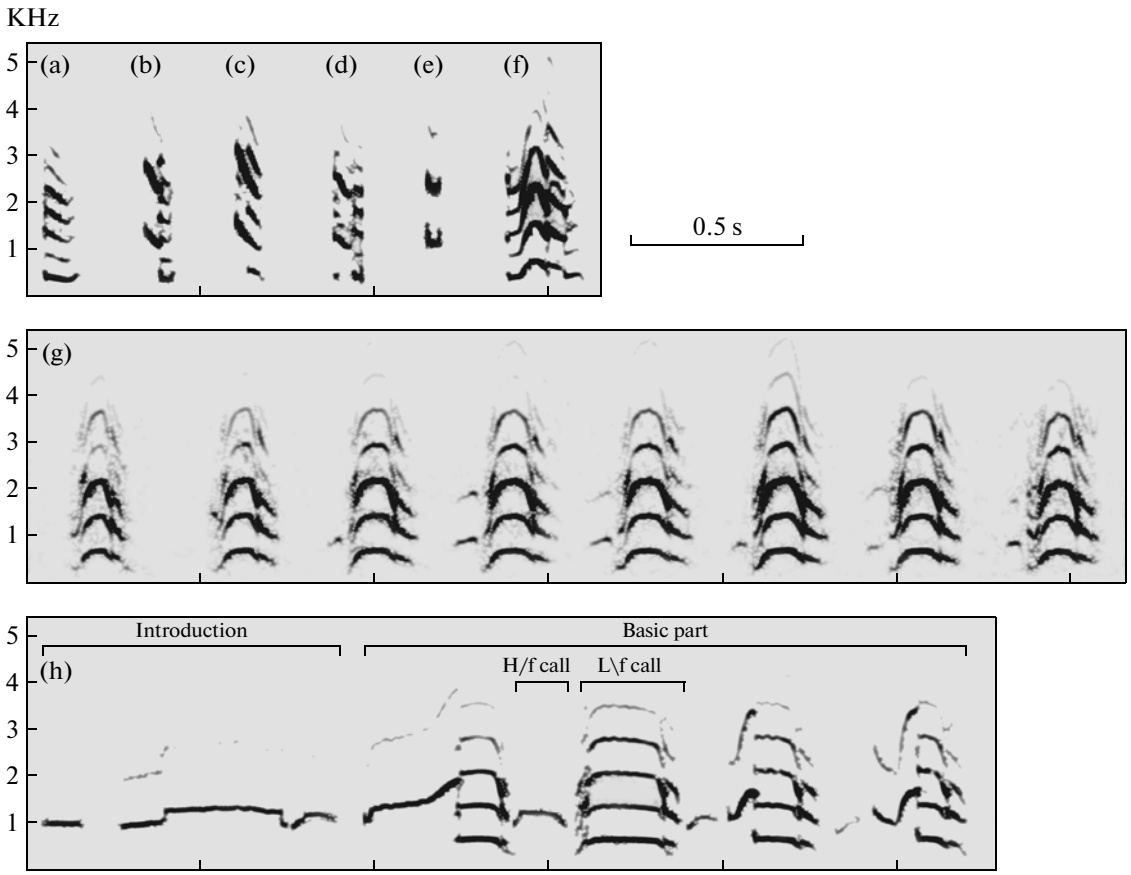

Fig. 4. Spectrograms of (a–e) babbling, (f) bark, (g) serial bark, and (h) trumpeting call of male crested auklet. In the trumpeting call, introduction (up to 1.0 s) consists of three high-frequency sounds, and the basic part (from 1.0 s to the end) consists of four low-frequency (l/f) and three high-frequency (h/f) sounds.

(Fig. 5f) in only 21.6% cases ($n = 250$). The total duration of the cackling sequence varied from 1.87 to 13.5 s, averaging 5.71 ± 2.0 s ($n = 119$); the average duration of introduction was 3.05 ± 1.67 s (n = 119); and that of the basic and final parts, 3.96 ± 1.33 s ($n = 80$).

Male–Female Differences in the Communicative Behavior of Crested Auklets

The communicative behavior of males and females in the crested auklets is similar in many ways. Thus, they devoted similar proportions of time to social activities: 22.8% in males ($n = 819$ min of records) vs. 19.9% in females ($n = 709$ min), with the difference lacking statistical significance ($p = 0.17$, White test). None of visual or acoustic displays observed in this study was characteristic of males or females alone. However, agonistic behavior and trumpeting displays were more frequent in males; consequently, they demonstrated communicative behavior twice as frequently as did females: 1.13 vs. 0.65 displays per minute (Fig. 6). Participation in the billing process was recorded slightly more frequently in females than in males, which could be explained by the fact that our observations were focused only on the behavior of the focal bird, without regard to the behavior of its partner.

Trumpeting displays were recorded in only two out of 22 females in 1990 and in one out of 21 females in 2008. In one of these three cases, the female displayed the trumpeting posture and call after the death of breeding partner; in another case, the breeding partner disappeared from the plot and failed to return until the end of observations. Widow females performed trumpeting displays very often, aggressively attacking neighboring auklets of either sex, although previously they had been regularly observed in billing with their breeding partners and had never assumed the trumpeting posture. This transformation of behavior is apparently explained by the loss of breeding partner and consequent loss of offspring, because both parents are necessary for successful egg incubation and chick rearing (Gaston and Jones, 1998; Fraser et al., 2002). Such a dramatic change in social conditions can lead to alterations in the hormonal profile of females, stimulating them for typical male displays.

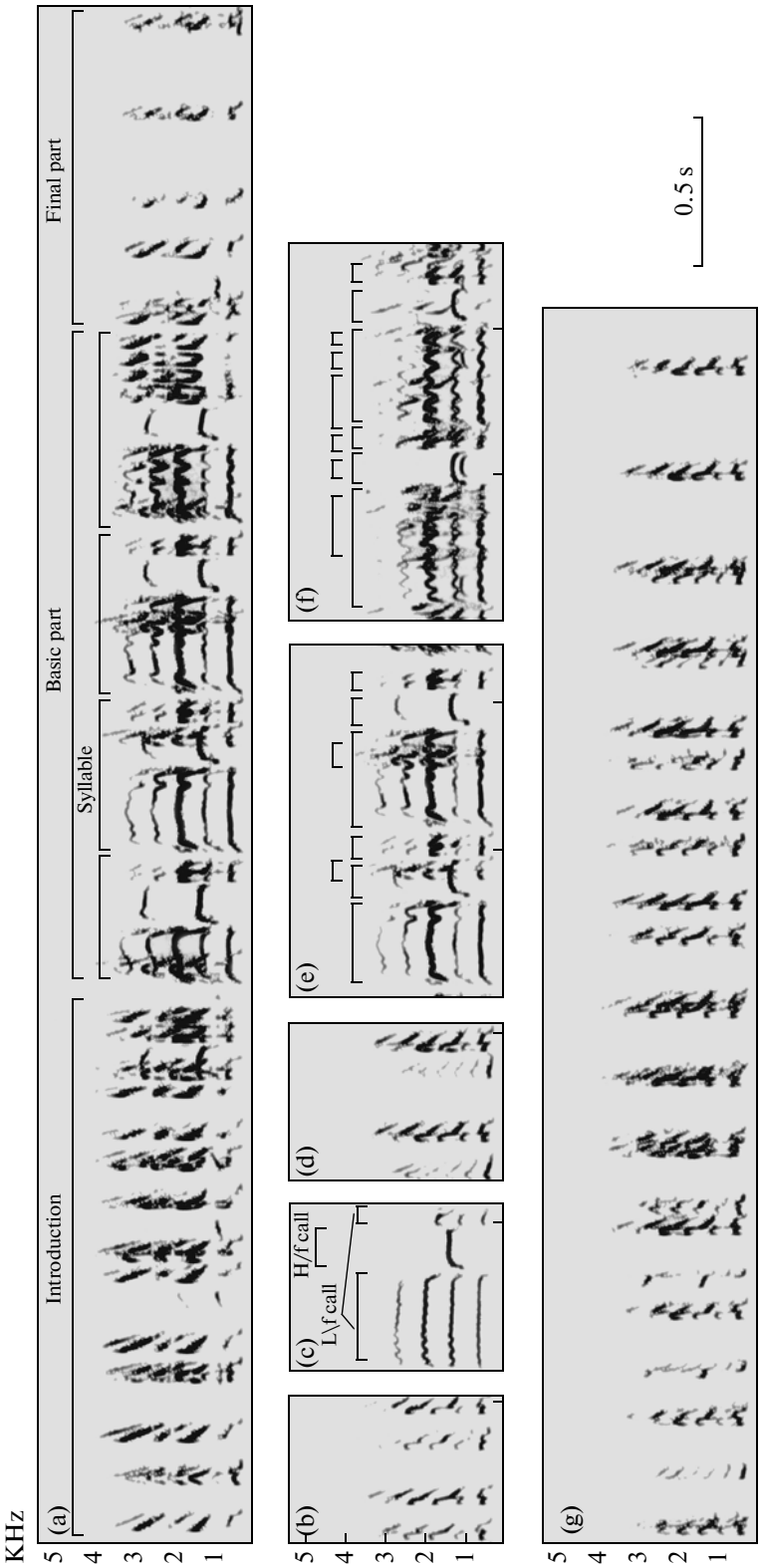

Fig. 5. Spectrograms of cackling of the crested auklet: (a) a complete cackling sequence of a male–female pair with introduction, the basic part consisting of four syllables, and the final part; (b) four sounds from the introduction; (c) one syllable from the basic part consisting of two low-frequency (l/f) and one high-frequency (h/f) sounds; (d) four sounds from the final part; (e) two syllables from the basic part of the sequence where one of the partners performs this part while the other emits introduction calls; (f) two syllables from the basic part of the sequence performed by both partners (horizontal lines indicate alternation of their voices); (g) incomplete cackling of two birds without the middle (basic) part.

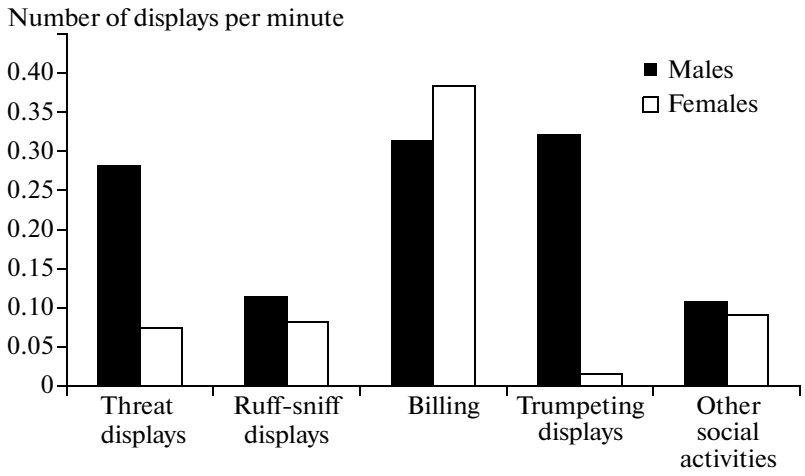

Fig. 6. Occurrence frequencies of different forms of communicative behavior in male and female crested auklets.

DISCUSSION

Studying the behavior of crested auklets at the surface of the colony in the breeding season, we have revealed ten postures and visual displays and five classes of sounds and vocal sequences. All types of visual and acoustic displays are characteristic of both males and females, with sex-related differences concerning mainly the frequency of their performance.

The results of our study confirm previous data on very high social activity of crested auklets either before or after pair formation (Zubakin, 1990; Jones, 1993; Gaston and Jones, 1998; Kharitonov, 2007). This activity is one of the most puzzling feature in the social behavior of this species. The functional significance of the vigorous and energy-intensive displays of crested auklets in the breeding season is not completely clear (Zubakin, 2007). It may well be that extra-pair consolidating displays ("club" pair formation) before the incubation period allow the birds to choose partners for extra-pair mating described in this species (Gaston and Jones, 1998; Hunter and Jones, 1999). Forced copulation in the crested auklet is impossible: mating takes place in the sea, and the male, having no copulatory organ, must hover over the female (Hunter and Jones, 1999). Therefore, the choice of the breeding partner is with the female.

Crested auklets are monogamous, and both partners are equally involved in incubating the single egg and rearing the chick (Gaston and Jones, 1998; Fraser et al., 2002). When not incubating, however, either partner continues self-advertisement and consolidation displays before other birds. The continuation of this activity after egg laying apparently allows these birds to find a pair for the next breeding season (Jones, 1993). This hypothesis is supported in part by the data that the composition of pairs in the crested auklet remains unchanged in the next season in only 45.5% of cases; in 25% of those pairs, both males and females return to the same colony but breed with different partners (Zubakin and Zubakina, 1993). However, reliable data on the connection between "club" pairing and the formation of breeding pairs in subsequent years are as yet lacking.

The crest is a distinctive detail of nuptial plumage that plays an important role in the communicative behavior of crested auklets during the breeding season, allowing the birds to estimate the quality of the potential sex partner (Jones and Hunter, 1999). Both males and females prefer birds with longer crests (Jones and Hunter, 1999). Interestingly, that similar preference was described in experiments with least auklets (*Aethia pusilla*) fitted with artificial crests, although these birds have no crest (Jones and Hunter, 1998). The origin of this preference is unclear, but the fact of its existence in the species that has no crest is evidence of key role of sexual selection in the evolution of this element of nuptial plumage in the crested auklet (Jones and Hunter, 1999).

The behavior of crested auklets shows certain similarity to the behavior of other auklets of the tribe Aethini. Conspicuous social activity in the breeding season on the surface of the colony has been described in all auklet species (Kharitonov, 1980; Byrd and Williams, 1993; Jones, 1993a, 1993c; Gaston and Jones, 1998; Jones et al., 2001). The only exception is the whiskered auklet (*Aethia pigmaea*): these birds are active at night in the greater part of the species range, and their social interactions largely take place in nest chambers and under stones (Zubakin and Konyukhov, 1999). Vocal repertoires of all auklet species include joint male–female displays accompanied by call sequences of both partners that are analogous to cackling of the crested auklet. These are "duet-whinneying" of the parakeet auklet (*Cyclorrhynchus psittacula*) (Jones et al., 2001; Seneviratne et al., 2009), "duet-chatter" of the least auklet (Jones, 1993c; Seneviratne et al., 2009), and "duet-beedoo" of the whiskered auklet (Byrd and Williams, 1993; Seneviratne et al.,

2009). All auklet species have by self-advertisement calls known as "whinneying" in the parakeet auklet (Jones et al., 2001; Seneviratne et al., 2009), "chatter" in the least auklet (Jones, 1993c; Seneviratne et al., 2009) and "beedoo" in the whiskered auklet (Byrd and Williams, 1993; Seneviratne et al., 2009). However, only the crested auklet has a self-advertisement call (the trumpeting call) structurally different from male and female vocalization during billing, while such calls in the whiskered, least, and parakeet auklets have the structure similar to that of duet-like vocalizations of pair partners (Byrd and Williams, 1993; Jones, 1993c; Jones et al., 2001; Seneviratne et al., 2009). Moreover, the parakeet and least auklets have no special trumpeting posture, and their billing displays look much simpler than that of the crested auklet (Jones, 1993c; Jones et al., 2001; Zubakin, personal communication).

The basic sound frequency in vocalizations of the crested and whiskered auklets is lower than 1.35 kHz (Byrd and Williams, 1993; Seneviratne et al., 2009), compared to 3–4 kHz in the parakeet and least auklets (Jones, 1993c; Jones et al., 2001; Seneviratne et al., 2009). The basic structural element of vocalization is a bark in the first two species (Byrd and Williams, 1993; Zubakin and Konyukhov, 1999; Seneviratne et al., 2009), and a trill in the parakeet and least auklets (Kharitonov, 1980; Jones, 1993c; Jones et al., 2001; Seneviratne et al., 2009). However, the self-advertisement (trumpeting) vocalization is a sequence of several calls corresponding to structural elements (barks or trills, depending on species). This vocalization in the crested auklet consists of barks alternating with high-frequency calls; in the parakeet auklet, of trills alternating with relatively soft low-frequency sounds (our unpublished data).

Therefore, irrespective of certain similarity, the communicative behavior of the crested auklet is more complex and diversified than that of closely related species. The difference is largely accounted for by elements of olfactory behavior and related postures and displays such as the touch and ruff-sniff displays. The crested auklet is the only species in the tribe Aethini and even in the whole family Alcidae in which olfaction has been proved to play a major role in social interactions (Hagelin, 2007; Hagelin and Jones, 2007; Rajchard, 2007). Evidently, the specific scent of crested auklets is no less important for their social status than is the nuptial plumage (Jones and Hunter, 1999; Hagelin et al., 2003; Jones et al., 2004). Whiskered auklets also have a specific scent in the breeding season, but its role in intraspecific communication remains obscure (Gaston and Jones, 1998; Douglas et al., 2004).

The unique scent of crested auklets probably has its source in the tiny wick feathers confined to a small patch of skin between shoulder blades, which have been shown to contain the highest concentrations of odorants (aldehydes) specific for these birds (Douglas, 2008). It appears that ruffling up the feathers on the nape and upper back during threat, trumpeting, and billing displays helps the bird to produce a cloud of scent around it, which attracts neighboring auklets and stimulated them for tactile interactions such as touch and ruff-sniff displays. This may account for scent transmission from one bird to another, primarily among partners in billing and close neighbors (Douglas, 2008), as is the case in highly social mammal species, e.g., the great gerbil (*Rhombomys opimus*) (Gol'tzman et al., 1977). Apparently, scent transmission within a local group of crested auklets allows the birds to distinguish trespassers from neighbors not only by acoustic and visual characteristics but also by scent, as in mammals, thereby reducing aggressiveness between the owners of neighboring territories. This is especially important when interactions take place not on the surface but in the dark depths of taluses where the nests are located. In all likelihood, scent communication will soon be revealed in the whiskered auklet, because birds of this species also have a specific scent in the breeding season (Douglas et al., 2004) and their social activities take place mainly underground and at night (Zubakin and Konyukhov, 1999).

Thus, the evolution of communicative behavior in the crested auklet has followed the pathway of its complication via increase in the diversity of acoustic and visual displays and development of chemocommunication as an additional modality.

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