

# Breeding vocalizations of the piping plover (*Charadrius melodus*): structure, diversity, and repertoire organization

Ha-Cheol Sung, Edward H. Miller, and Stephen P. Flemming

**Abstract:** We studied breeding vocalizations and the vocal repertoire of the endangered piping plover (*Charadrius melodus* Ord, 1824) to describe diversity of the species' non-learned vocalizations, provide a basis for comparative studies, and enable standardization of terminology and interpretation of vocal classes for management purposes. Adults have 14 call types and newly hatched chicks have three; these are underestimates of repertoire size because they represent breeding vocalizations only and are biased toward loud, easily recorded sounds. Vocalizations are structurally diverse: duration, ~10 ms to 1.5 s; peak frequency (adults), <900 to >3000 Hz; tonal to pulsed or noisy; narrow- to broad-band; and nonharmonic to harmonic. Vocalizations are higher in frequency in females than in males. High vocal diversity results from differential combination and sequencing of fairly simple acoustic attributes such as pulsing and frequency modulation, and from quantitative variation in such attributes. Homologies with other species of Charadriidae in acoustic traits of calls, call types, and organization (syntax) within calls and across call types are suggested. Acoustic characters at different organizational levels are highly conserved evolutionarily; hence, they seem to hold promise for phylogenetic analyses within the family.

**Résumé :** Nous avons étudié les vocalises de reproduction et le répertoire vocal du pluvier siffleur (*Charadrius melodus* Ord, 1824), une espèce menacée, afin de décrire la diversité des vocalises non apprises de l'espèce, de fournir une base pour les études comparatives et d'établir une standardisation de la terminologie et de l'interprétation des classes vocales à des fins d'aménagement. Les adultes possèdent 14 types d'appels et les poussins fraîchement éclos trois; il s'agit d'une sous-évaluation de la taille du répertoire, car nous considérons seulement les vocalises de reproduction et il y a une prédominance de sons forts, faciles à enregistrer. Les vocalises diffèrent par leur structure: durée de ~10 ms à 1,5 s, fréquence maximale (adultes) de <900 à >3000 Hz, tonales à pulsées ou bruyantes, à bande étroite ou large, non harmoniques à harmoniques. Les vocalises des femelles ont des fréquences plus élevées que celles des mâles. L'importante diversité vocale résulte de combinaisons différentielles et de mise en séquence d'attributs acoustiques relativement simples, tels que la pulsation et la modulation de fréquence, ainsi que de la variation quantitative de ces attributs. Nous suggérons certaines homologies avec d'autres espèces de Charadriidae dans les caractères acoustiques des appels, les types d'appels et l'organisation (syntaxe) dans un même appel et entre les appels. Les caractéristiques acoustiques aux différents niveaux d'organisation sont fortement retenues au cours de l'évolution; il semble donc y avoir une possibilité de faire des analyses phylogénétiques au sein de cette famille.

[Traduit par la Rédaction]

## Introduction

Social signals such as acoustic displays can diverge rapidly in isolated populations, especially mating signals under the influence of sexual selection (Coyne and Orr 2004). Nevertheless, bioacoustic characters have long been used in systematic studies of acoustic insects, anurans, mammals, and birds, indicating that some displays (even learned displays) evolve slowly enough to be phylogenetically infor-

mative (Lanyon 1969; Payne 1986; Zimmermann 1990; Macedonia and Stanger 1994; Irwin 1996; McCracken and Sheldon 1997; Price and Lanyon 2002; Raposo and Hoefling 2003; Montealegre-Z and Morris 2004); indeed, some acoustic attributes are shared by shorebird taxa that diverged from one another millions of years ago (Miller 1996). Overall, phylogenetic reconstruction using bioacoustic traits has met with only mixed success; more promising uses of bioacoustic information in systematics are in determining patterns

Received 16 September 2004. Accepted 23 March 2005. Published on the NRC Research Press Web site at <http://cjz.nrc.ca> on 14 June 2005.

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and rates in display evolution within phylogenies established on other bases, such as molecular data (Price and Lanyon 2002; Desutter-Grandcolas 2003; Paeckert et al. 2003).

In systematics, choice and description of characters are made over multiple scales, as appropriate to the entities (operational taxonomic units, clades, etc.) under investigation (e.g., presence/absence of feathers versus specific attributes of feathers; Sneath and Sokal 1973; Wiley 1981; Mayr and Ashlock 1991). Descriptions of animal displays and statements about homology follow the same principle over structural scales such as song syllables, song or call types, call-type sequences, and higher order structures (Kroodsma 1982; Smith 1986, 1991, 1996, 1997; Bain 1992; Hall 1994; Desutter-Grandcolas 2003; Nelson 2004). It seems likely that evolution proceeds at different rates on different organizational levels, but this has not been investigated for animal displays, to our knowledge. Information about display structure and variation, the display repertoire, and behavioural significance of displays is a necessary first step for understanding hierarchical organization and relationships among display entities.

Structural organization of avian vocalizations has been investigated mainly for learned song in Oscines. Essentially no such work has been done on non-learned vocalizations of other taxa, which may evolve more slowly (and hence may be more phylogenetically informative) and for which evolutionary patterns may differ; simple syringeal anatomy may constrain vocal complexity or limit diversification of call types within the repertoire, for example. Non-learned vocalizations characterize the monophyletic Charadriiformes (shorebirds, gulls, auks, etc.), a large, diverse, and ancient group that diverged from other birds in the Late Cretaceous Epoch, ~80 Ma BP (Miller 1984, 1992, 1996; Piersma 1996; Wiersma 1996; Paton et al. 2002). Divergences within the Charadriiformes also are deep; the clade containing plovers and lapwings (Charadriidae; 67 species) arose in the Oligocene Epoch (~32 Ma BP), and currently recognized genera diverged within the clade soon after (Paton et al. 2003). The antiquity and taxonomic complexity of Charadriiformes, and their diverse displays and loud vocalizations, make the group attractive for investigating display evolution.

To advance knowledge of vocalizations in Charadriidae for comparative purposes, and to provide tools for conservation and management (e.g., to standardize observational protocols, terminology, and interpretation across observers; Nebel and McCaffery 2003), we studied vocalizations of the piping plover (*Charadrius melodus* Ord, 1824), an endangered endemic North American species and one of 32 species in the genus *Charadrius* (Haig 1992; Haig and Elliott-Smith 2004). Vocal individuality will be described elsewhere. Here we describe structure of vocalizations and the vocal repertoire, make comparisons with related species, and propose some vocal homologies.

Nomenclature for common and scientific names follows Wiersma (1996), except the widespread species *Charadrius alexandrinus* L., 1758 is referred to as Kentish plover unless the western North American (*C. a. nivosus*) or South American (*C. a. occidentalis*) subspecies are specified, in which case the names western snowy or Peruvian plover (respectively) are used (Sibley and Monroe 1990; Page et al. 1995; American Ornithologists' Union 2004).

## Materials and methods

We studied plovers at the following three sites: (1) Cape Ray Cove, Cheeseman Provincial Park, Newfoundland and Labrador (47°37'N, 59°16'W), 1–15 May 1999; (2) Summit Creek area of Lake Diefenbaker, Saskatchewan (50°59'N, 106°29'W), 11–18 May 2004; and (3) Prince Edward Island National Park (PEINP), 1 May – 30 July 1998 and 17 May – 15 July 1999. Most observations and recordings were made at PEINP. We include spectrograms of calls recorded by W.W.H. Gunn at Long Point, Ontario (a former nesting site for the species) in July 1963 (Macaulay Library of Natural Sounds (MLNS), Cornell University, Ithaca, New York, catalogue No. 62327). We also analyzed calls of *C. a. nivosus* recorded by G.A. Keller at Coos Bay, Oregon (July 1994; MLNS 105498); *C. a. occidentalis* recorded by T.A. Parker III near Ica, Peru (July 1982; MLNS 23961); common ringed plover (*Charadrius hiaticula* L., 1758) recorded by B.N. Veprintsev near Uelkal, Chukotka, Russia (June 1977; MLNS 92026, 92787); and semipalmated plover (*Charadrius semipalmatus* Bonaparte, 1825) recorded by D.R. Gunn at Frobisher Bay, Baffin Island, Nunavut (July 1961; MLNS 62328, 62330, 62333) and E.H.M. in northwestern British Columbia ("Haines Triangle"; June 1983).

PEINP was divided into four study areas: Cavendish (46°30'N, 63°25'W), Brackley Beach (46°25'N, 63°13'W), Blooming Point (46°24'N, 62°59'W), and Greenwich (46°27'N, 62°39'W). The Cavendish area included Cavendish Sandspit and North Rustico Beach, and the Brackley Beach area included Rustico (Robinson's) Island Sandspit, Rustico Causeway, and Covehead Beach. Each area was 4–7 km long and included beaches of various sizes. Cavendish Sandspit, Rustico Causeway, and Blooming Point Sandspit included nesting habitat in cobble washthroughs and a dynamic dune system. Nesting areas were closed to human recreational use during nesting and chick rearing.

Observations and audio recordings were made opportunistically at sites 1 and 3. Observations at PEINP were made from 0600 to 1200 and for 4 h before sunset each day. Most observation periods were 1 h in duration. Observations were made from behind well-developed dunes at distances of >20 m, using 7 × 35 binoculars and a 20 × 60 spotting scope. Following Simmons (1955), we lay or sat motionless for >15 min before beginning observations. This method was especially effective during the period of pairing, and several pairs performed seemingly normal courtship behaviour only ~10 m from observers. At visits to each site, vocalizations were sampled in several ways. First, we recorded calls from apparently undisturbed focal birds on an ad hoc basis during observation periods. Second, we waited until targeted individuals were vocally active and then recorded particular call types. Third, between observation periods, we recorded vocalizations opportunistically as we walked between observation posts. Finally, around hatching, we recorded calls of chicks and parents by the nest.

Call types varied greatly in audibility (e.g., brooding versus display-flight calls) and recordability (e.g., "alarm" calls of nearby standing birds versus calls in rapid aerial chases), so it was not possible to quantify proportional occurrences or contextual uses of different call types from our data. H.-C.S. and E.H.M. independently analyzed all recordings and agreed on

most call classifications. Some disagreements resulted in the recognition of two heterogeneous call types (A9, A11).

Except for recordings of calls by parents and chicks around hatching, audio recordings were made with a Sony TC-D5PROII tape recorder and Telinga Pro-4 parabolic microphone with flexible parabolic reflector (Telinga Microphones, Tobo, Sweden) or (in Saskatchewan) with the same microphone and parabolic reflector plus a Marantz PMD670 solid-state recorder (sampling rate 44.1 kHz). Vocalizations of chicks with their parents were recorded by placing a dynamic microphone (model 2302, Turner Co., Cedar Rapids, Iowa) about 1 m from nests, connected to the Sony tape recorder by a long cable. The recorder was hidden by beach debris or a dune. Observations were made simultaneously with audio recordings beginning ~10 min after the start of recording, from distances of >20 m and from behind dunes. If parents appeared to be disturbed, recordings and observations were terminated.

Sex of birds was judged by behaviour and external features, including extent and darkness of plumage of the forehead and breast, plus bill colour (Haig 1992; Haig and Elliott-Smith 2004). Markings on the forehead and breast are darker and more extensive in males than in females, and orange on the bill of males is richer and more extensive (i.e., the black tip on the bill is smaller) than in females (the black tip on the female's bill was usually >50% of bill length).

Calls were analyzed with Raven 1.1 or 1.2 software (MLNS) or CSL 4300 or MultiSpeech 3700 software (Kay Elemetrics, Pine Brook, New Jersey). Most measurements were made on well-sampled call types from PEINP only, after digitization of recordings at 25 kHz; some measurements of Saskatchewan samples were also made, as described below (digitization at 44.1 kHz). Variables measured on spectrograms were as follows (as applicable): total call duration; intercall interval; duration of call part; interval between call parts; and dominant frequency. For A1a calls, total call duration and intercall intervals excluded introductory pulsing, which was often indistinct owing to variable quality of recordings (e.g., see Fig. 4A in Haig 1992; Haig and Elliott-Smith 2004). We used a frequency range of 600–6000 Hz with an effective filter bandwidth of 72 Hz for measuring temporal variables; dominant frequency in each call was estimated in CSL as the energy peak on a power spectrum computed with window size = 512 points, Blackman window weighting, and low smoothing. Spectrograms shown below were prepared to be comparable with one another as much as possible, but some variation is present because of different call-type properties or to emphasize points of interest. For samples digitized at 44.1 kHz (i.e., all except those from Prince Edward Island), spectrograms were prepared with window size = 325 points, frame overlap = 90%, frequency grid spacing = 86 Hz, and Blackman window weighting (the exception was the spectrogram shown in Fig. 2K: 200 points, 95% overlap, grid spacing 86 Hz, and Blackman weighting). For comparable spectrograms, corresponding settings for the Prince Edward Island samples digitized at 25 kHz were 185 points, 90% overlap, 86 Hz, and Blackman weighting. For graphical purposes, we grouped call types as spectrograms by appropriate frequency range for analysis; hence, figures do not simply follow the order of description under Results.

## Results

We recognized 17 classes of vocalization on mainly structural grounds: 14 for adults (A1 to A14) and three for chicks (C1 to C3). Some classes are heterogeneous and could be split further (e.g., A9). We introduce each class with observations on contextual and seasonal use, then describe pattern of delivery, structure, and variation, following Smith (1986, 1991, 1996, 1997).

### Adult call type 1a (A1a), used in butterfly flights (Figs. 1A–1C)

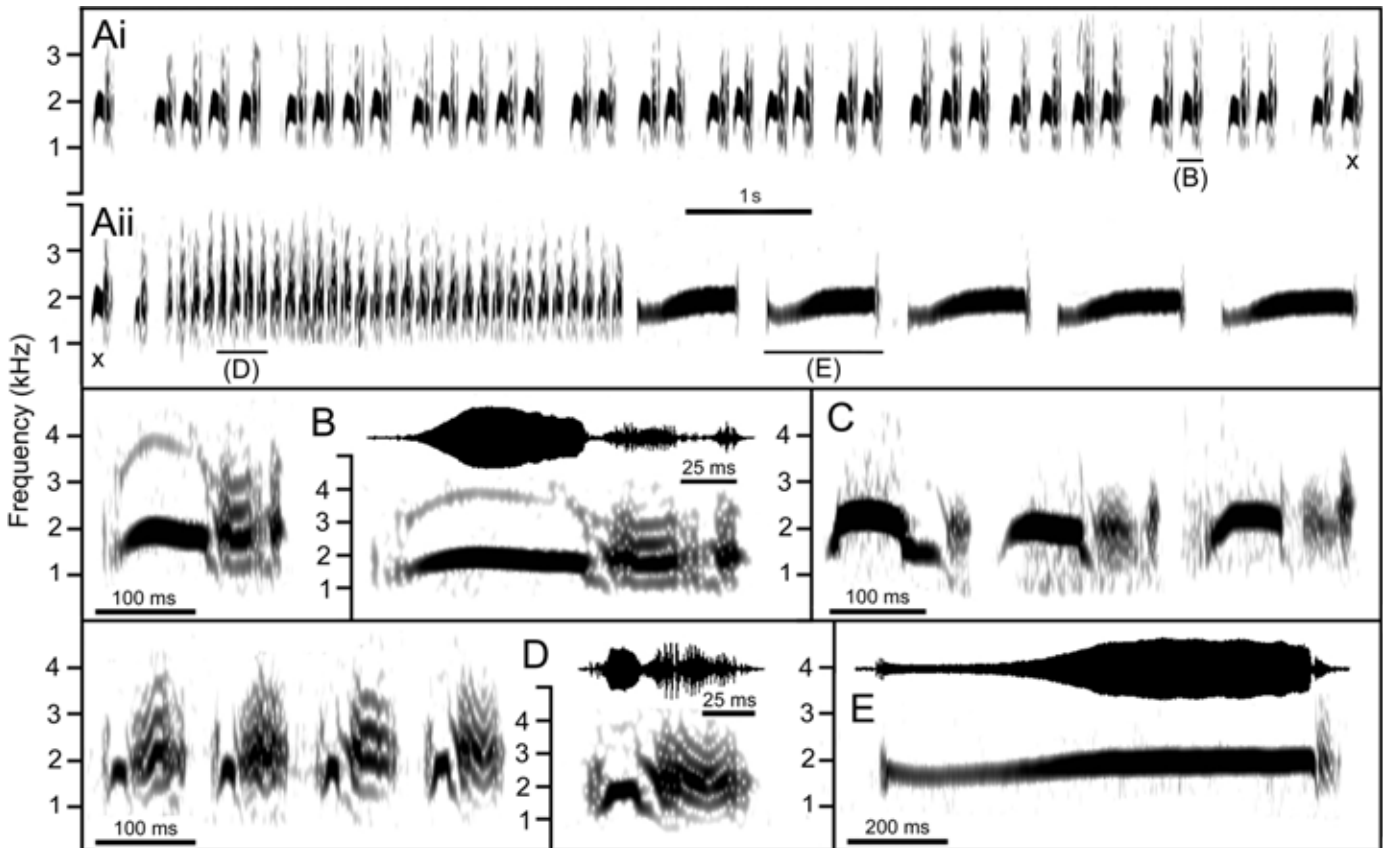
The loud, stereotyped version of this call was given during aerial display flights (“butterfly flights”, BFs hereafter; Cairns 1977, 1982; Haig 1992; here and below also see Haig and Elliott-Smith 2004) over or near future nesting territories or females (even distant from future nesting sites), or during pauses within lengthy bouts of agonistic or courtship interactions on the ground. It also was uttered from the ground before or following BFs, from the ground in response to passing birds, etc. Several birds often chased one another or displayed close to one another during simultaneous BFs; females participating in these aerial mêlées did not utter A1a calls. Birds often uttered A3 or A4 calls on the ground before initiating BFs. During BFs, A3 (or A4 or A7) calls interrupted A1a call series occasionally. A3 or A4 calls also were uttered by birds in descent or after landing from BFs, and A1a call series were given after landing.

BFs were performed by unpaired or recently paired territorial males, renesting males, or (less commonly) males attending chicks. Territorial males gave this display in response to activities of other males (e.g., nest-scraping behaviour by intruder, nearby BF). Renesting males gave this display in response to passing individuals (males defended territories until mid-July). Males interrupted BFs to chase other species, including rock dove (*Columba livia* Gmelin, 1789) and killdeer (*Charadrius vociferus* L., 1758). Single BFs lasted from <1 min to ~30 min, but some BF bouts lasted several hours, punctuated by brief periods of rest on the ground.

In the prenesting period, males commonly terminated BFs near females and began nest-scraping displays. BFs often were followed or preceded by territorial interactions with neighbours, including ground chases, parallel running, or brief fights, incorporating A3, A4, or A7 calls. During their mates' aerial displays, females were silent or moved within the territory, sometimes uttering A9 or A12 calls.

A1a calls were uttered in long, rhythmic series at a rate of 4–5 calls/s; calls averaged ~165 ms with intercall intervals of ~65 ms, for a duty cycle of 0.72 (Table 1; Fig. 1Ai). Calls were highly stereotyped but some variation occurred as gradual changes in duration, repetition rate, or frequency, particularly at the start or end of a calling sequence (successive grading or “drift”; Andrew 1969; Lemon 1975; Marler 1976; Miller 1979). For example, frequency was low during slow calling and then, following long intervals within bouts, increased with calling rate. Pulses preceded the call in most males (Fig. 1B) and were followed by the longest part of the call, which was tonal, harmonically weak, and high in amplitude, increasing from ~1.5 to ~2.3 kHz within ~30 ms before decreasing quickly (sometimes abruptly) in frequency;

**Fig. 1.** Nuptial vocalizations of piping plovers (*Charadrius melodus*). (A) Sequence of A1a-A4-A3 calls given by males in butterfly flight (Saskatchewan); natural intercall intervals are shown. The sequence is split between upper and lower parts of the panel; “x” marks the same call in both parts. Letters in parentheses indicate parts that are analyzed further in panels B, D, and E. (B) Single A1a call from panel A shown as spectrogram (left) and waveform plus spectrogram (right) on different timescales. (C) Single A1a calls from three different males in butterfly flight (Prince Edward Island). (D) Four A4 calls from panel A shown as spectrogram (left); natural intercall intervals are shown. Last call is shown also as waveform plus spectrogram (right) on a different timescale. (E) Single A3 call from panel A shown as waveform plus spectrogram.



amplitude varied directly with frequency (Fig. 1B, right). Sometimes the tonal part changed (following a sharp frequency shift) to a low-amplitude, declining-frequency, tonal segment with or without strong harmonics and complex pulsing (Fig. 1B, first two calls in Fig. 1C). Calls ended with one to several pulsed sections (pulse rates up to several hundred Hz) that differed across individual birds (Figs. 1B, 1C).

The A1a call was termed an “aerial courtship call” by Haig (1992), and has been described variously as *kuk-kuk-kuk* (Pickwell 1925), *bec-bec-bec* (Cairns 1977), and *pipe-pipe-pipe* (Haig 1992).

#### Adult call type 1b (A1b), used in copulation and scraping displays (Figs. 2A, 2B)

Calls similar in structure to A1a calls were given in another, distinctively different situation. We categorized them as A1 calls because of their strong structural similarity to A1a calls and their organization in long rhythmic sequences. The central part of the call was tonal with a simple, relatively slow increase to a peak, followed by a slow decrease; usually no harmonics were evident. The tonal portion was introduced and terminated by simple pulsing.

A1b calls were given by males during copulation, bouts of ground courtship, or nest-scraping displays (e.g., when a

male was alone by a scrape). Calls given by lone scrape-displaying males were audible over long distances on calm quiet days and were uttered rhythmically in long series at a rate of  $\sim 3/s$ , punctuated several times per minute by A2 call series, then continuing. (Haig (1992) also noted the association and distinction between A1b and A2 call types.) A1b calls intergraded into A1a calls during the tilt display of displaying males (Cairns 1982).

#### Adult call type 2 (A2) (Figs. 2A, 2B)

A2 calls occurred only in nest-scraping displays, typically embedded within series of A1b calls. They were uttered as series of 10–15 successively graded brief calls, increasing over the series from  $\sim 20$ – $25$  to  $\sim 40$ – $45$  ms in duration, with a total series duration of  $\sim 1$ – $2$  s. Each call was tonal and lacked evident harmonics, with a simple increase then decrease in frequency (main frequency  $\sim 1.8$ – $2.1$  kHz); some terminal pulsing was present.

A2 calls usually were associated with the digging phase of the nest-scraping display (Haig 1992).

#### Adult call type 3 (A3) (Figs. 1Aii, 1E)

This call type was given by both sexes from the ground (mainly by males) and by males in BFs. A4 calls usually

**Table 1.** Summary of descriptive statistics for measured variables<sup>a</sup> of vocalizations of breeding adult piping plovers (*Charadrius melodus*) recorded in Prince Edward Island National Park, 1998–1999.

Call types and variables	Grand mean ± SD ( <i>n</i> = no. of birds)	Range of individual means ( <i>n</i> = no. of birds)	Range of total calls ( <i>n</i> = no. of calls)
<b>A1a</b>	<i>n</i> = 9	<i>n</i> = 9	<i>n</i> = 382
Duration, tonal part	93±14	77–116	56–136
Duration, terminal pulsing	22±2	19–24	16–32
Interval, start to peak F, <sup>b</sup> tonal part	29±5	26–36	10–44
Duration, total <sup>c</sup>	163±14	144–197	103–221
Intercall interval <sup>d</sup>	65±24	36–104	27–197
Dominant F, tonal part	2155±124	1927–2339	1784–2441
Dominant F, terminal pulsing	2356±217	1933–2523	1750–2912
<b>A2</b>	<i>n</i> = 2	<i>n</i> = 2	<i>n</i> = 59, 59, 52 <sup>e</sup>
Dominant F	2162±150	2079–2211	1683–2441
Duration, total	30±5	28–32	17–47
Intercall interval	124±25	113–143	74–199
<b>A3</b>	<i>n</i> = 21, 18 <sup>e</sup>	<i>n</i> = 21, 18 <sup>e</sup>	<i>n</i> = 248, 148 <sup>e</sup>
Dominant F	1944±104	1691–2064	1592–2138
Duration, total	776±162	577–1083	100–1280
<b>A7</b>	<i>n</i> = 36	<i>n</i> = 36	<i>n</i> = 1376, 1376, 1273 <sup>e</sup>
Dominant F	2577±129	2312–2868	2003–3030
Duration, total	65±10	48–83	39–108
Intercall interval	360±110	188–566	14–975
<b>A9</b>	<i>n</i> = 21	<i>n</i> = 21	<i>n</i> = 661
Dominant F, tonal part	1577±318	1232–2141	875–2340
Duration, total	101±24	65–137	42–170
<b>A10</b>	<i>n</i> = 11	<i>n</i> = 11	<i>n</i> = 152
Dominant F	1919±176	1630–2171	1531–2441
Duration, total	101±45	63–173	57–210
<b>A11</b>	<i>n</i> = 51	<i>n</i> = 51	<i>n</i> = 1426
Dominant F	2653±108	2464–2893	2340–3164
Duration, part	157±35	97–216	72–412
<b>A12</b>	<i>n</i> = 42	<i>n</i> = 42	<i>n</i> = 589
Dominant F, 1st part	2386±373	1550–2743	1144–2912
Duration, 1st part	90±20	65–157	39–207
Interpart interval	70±28	22–114	19–228
Dominant F, 2nd part	2056±338	1299–2419	824–2508
Duration, 2nd part	91±51	51–241	25–331
<b>A14</b>	<i>n</i> = 11	<i>n</i> = 11	<i>n</i> = 31
Dominant F	2204±185	1885–2359	1851–2474
Duration, total	373±75	266–434	255–505

<sup>a</sup>Units are ms or Hz, as appropriate.

<sup>b</sup>F, frequency.

<sup>c</sup>Excluding introductory pulsing. Haig (1992, p. 5) estimated “overall duration” at 160 ms.

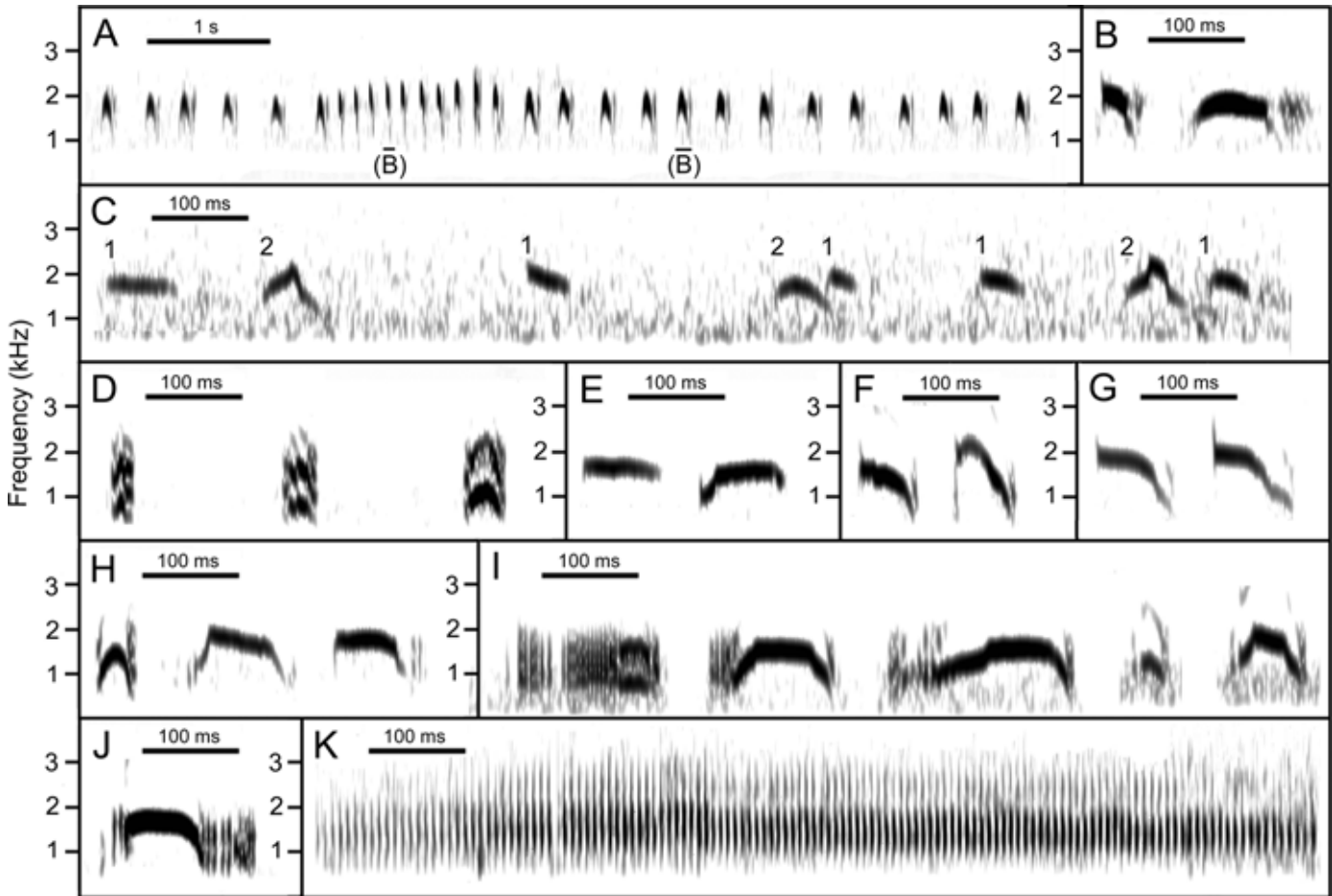
<sup>d</sup>End of terminal pulsing to beginning of tonal part of following call. Haig (1992) estimated intervals at 60 ms.

<sup>e</sup>Respective sample sizes for variables.

preceded this call type when calling was directed toward heterospecific or conspecific birds on the ground (accompanied by horizontal threat display, HTD; Cairns 1977). This was one of the most frequently heard calls during the breeding season and was given in five general contexts. (1) The call was used during attempted copulations. One pair member used this call while approaching the mate. In addition, one female gave this call intermittently without showing any interest in the male’s repeated courtship attempts when a red

fox, *Vulpes vulpes* (L., 1758), was nearby. (2) It was elicited by the approach of conspecific birds or predators (including humans) toward the nest. It was given also after a bird near its nest heard A1a or A12 calls. (3) It was used in hostile encounters on neutral areas, such as small puddles used for bathing or feeding; interacting birds called while in HTDs. (4) A3 calls were used by males when moving between nest-scraping locations. One male gave A3 calls as he returned to the nest to relieve his mate in incubation. (5) A3

**Fig. 2.** Nuptial vocalizations (concluded) and variable short-range vocalizations of the piping plover. (A) Portion of very long (>10 min) vocal sequence in nest-scraping display by lone male, showing an A2 call (with rapidly repeated elements) embedded in a long series of A1b calls; natural intercall intervals are shown (Saskatchewan). Letters in parentheses indicate parts that are analyzed further in panel B. (B) Single A2 element (left) and single A1b call (right) from panel A, shown as spectrograms on different timescales. (C) A9 calls uttered by two birds (1, 2) during agonistic interactions on the ground; natural intercall intervals are shown (Prince Edward Island). (D–J) A9 calls uttered by seven different undisturbed adults with chicks at nests on day of hatching. Calls in panel D were uttered as a triplet (natural intercall intervals are shown); calls in panels E–I are not in sequence. (K) Soft A5 call uttered by an adult in an agonistic interaction on the ground (Saskatchewan).



calls were used when receivers were engaged in inappropriate behaviour (e.g., parents uttered A3 calls when chicks were moving instead of crouching motionless in the presence of a nearby predator).

A3 calls were repeated rhythmically in series, with intercall intervals of ~250–500 ms (Fig. 1Aii). Calls were of moderate amplitude and were long and of narrow bandwidth, rising in frequency (with coupled amplitude) gradually from ~1.3 to ~2.2 kHz, then declining abruptly at the end; usually no harmonics were evident. Amplitude varied directly with frequency (Fig. 1E). Each call began and ended with a pulsed section (Fig. 1E). A3 calls have been described as *whooaah whooaah* (Pickwell 1925), *queep-queep-queep* (Cairns 1977), and *woo-up, woo-up* (Haig 1992).

#### Adult call type 4 (A4) (Figs. 1Aii, 1D)

Adults of both sexes (but mainly males) uttered A4 call series throughout the breeding season. Males often uttered them during BFs. On the ground, birds called while in HTD toward receivers in varied agonistic contexts, with fluffed body plumage and wings held away from the body. The calls

were directed toward trespassing shorebirds of similar size or toward the mate or chicks when they showed seemingly inappropriate behaviour (see above). A4 calls often were associated with A1a and A3 calls.

A4 calls were brief and uttered rapidly (~8/s; Fig. 1Aii) in rhythmic series. Calls usually increased in frequency, amplitude, and duration over a series. The first portion of the call was tonal and lacked evident harmonics; pulsing at the minimum frequency occurred in the centre of the call (Prince Edward Island only) or after the tonal portion (terminal pulsing may be longer in Saskatchewan). The basic pattern of [introductory pulsing – tonality (weak harmonics) – downward frequency shift – terminal pulsing] parallels the organization of A1 calls.

Cairns (1977) described this call type as a series of low, rattling *bec-bec-bec* calls.

#### Adult call type 5 (A5) (Fig. 2K)

This call type was heard rarely and recorded only once. It was uttered in agonistic interactions on the ground. The recorded series of six calls was given by a male that had

landed from a BF: he uttered the A5 series then rushed at the other bird, which flew away. It was a soft pulsed call that sounded like a quiet growl, repeated in series. The six recorded calls averaged  $1.17 \pm 0.15$  s long with pulse rates of  $27.8 \pm 1.47$  Hz; intercall intervals ( $n = 5$ ) averaged  $716 \pm 85.9$  ms long. They were fairly broad in bandwidth ( $<1$  to  $>3$  kHz), with most energy at 1–2 kHz.

#### Adult call type 6 (A6) (Fig. 5D)

One sequence of this call type was recorded during an agonistic ground interaction, though it was heard on other occasions. It was a sequence of harsh-sounding, rhythmically repeated calls, broad in bandwidth owing to rich harmonic structure, and with complex frequency modulations. Calls in the series illustrated (plus two preceding calls, not shown, for  $N = 10$ ) averaged  $117.7 \pm 3.06$  ms long, with intercall intervals of  $42.6 \pm 2.59$  ms.

#### Adult call type 7 (A7) (Figs. 3A–3F)

With brief A11 calls (and intergrades between the two call types), this is the call type after which the species is named. A7 calls were given mainly in three contexts. (1) The call was directed toward conspecific birds during the prenesting period, especially during the period of competition for territories. It was elicited when an individual or group of birds (of this species, sometimes mixed with other shorebirds) foraged near the territory. The responding bird (usually a territorial male) flew toward the other birds while uttering A7 calls. After landing, the male continued to call with erect postures and head bobbing, followed by the parallel-running display. In addition, the calling male continued to chase the other birds with HTDs while uttering other calls, including A3 and A4. Ground chasing often merged into aerial chasing. Similar behaviour was observed in newly arrived adults (e.g., two probable pairs in prospective nesting areas). The pairs repeatedly performed behaviour like that described above (plus some fights) over several hours. (2) As a warning to chicks, the call was used by both members of a pair during the period of chick care. Birds called when they saw potential predators approaching on the ground near the chicks (including humans and common raven, *Corvus corax* L., 1758); calling continued until the predators left. Chicks responded to this call by crouching motionless or moving in a stop-and-run manner from feeding to hiding places. Calling birds appeared to direct A7 calls to their chicks, simultaneously making themselves conspicuous to the predators. Calls uttered in this context sounded longer than in context 1. (3) Birds uttered this call type when approached by humans at all stages of the breeding cycle.

A7 was repeated in brief to long, approximately rhythmic series (Figs. 3A, 3E). Successive intergrading occurred especially at the beginning or end of a calling sequence, when calls were longer (Figs. 3C, 3D). A7 calls were brief and fairly high in frequency, and harmonics were weak (Figs. 3A–3F). Onset and offset were sudden but often spanned a considerable frequency range. A distinctive feature of some sequences was a sudden shift in frequency between successive calls, with changes in the reverse direction one to several calls later; multiple reversals also occurred (Figs. 3E, 3F).

Frequency differed significantly between the sexes: 2.55 Hz in males, 2.63 Hz in females (H.-C.S., unpublished data).

#### Adult call type 8 (A8) (Fig. 5C)

During agonistic interactions some brief calls were uttered singly, as couplets, or rarely as triplets. Each call rose sharply in frequency which, combined with the presence of harmonics, resulted in broad bandwidth.

#### Adult call type 9 (A9) (Figs. 2C–2J)

For practical purposes we distinguished this heterogeneous and probably unnatural class of vocalizations as brief, low-amplitude calls given by adults in short-term social interactions. These calls were uttered over short distances by parents attending or brooding chicks, or during approach to or departure from the nest or brood. A9 calls also were given during ground courtship or in interactions with neighbouring or unknown adults. A12 calls were used in similar contexts. Countercalling typified social interactions between adults, and females often uttered A9 calls in response to courting males.

A9 calls were given at irregular, brief intervals but in some contexts were uttered rhythmically as couplets or short bouts, notably by brooding birds. They were brief and low in amplitude but otherwise varied widely in structure. At their simplest, they were tonal, with weak harmonic structure, and displayed simple changes in frequency (Figs. 2C, 2E–2H). Others had quasi-rhythmic frequency modulation or strong harmonic structure (Fig. 2D). Like some call types described above, A9 calls often were preceded by a brief pulsed part followed by silence or were pulsed at the beginning (Figs. 2F–2J). A common and fairly stereotyped form of A9 calls was given by brooding birds: compound, with pulsing at the start and end, the main part of the call being tonal with no evident harmonics (Figs. 2I, 2J). The resemblance to A1 calls may reflect the intense excitement at this time; so-called nuptial vocalizations are given even by female least sandpipers (*Calidris minutilla* (Vieillot, 1819)) brooding chicks on the day of hatching (Miller 1985). Many variations in duration and other features of A9 brooding calls occurred; pulsed sections occurred with simple tonal calls, and pulsed utterances sometimes occurred independently (e.g., first call in Fig. 2I).

#### Adult call type 10 (A10) (Fig. 5A)

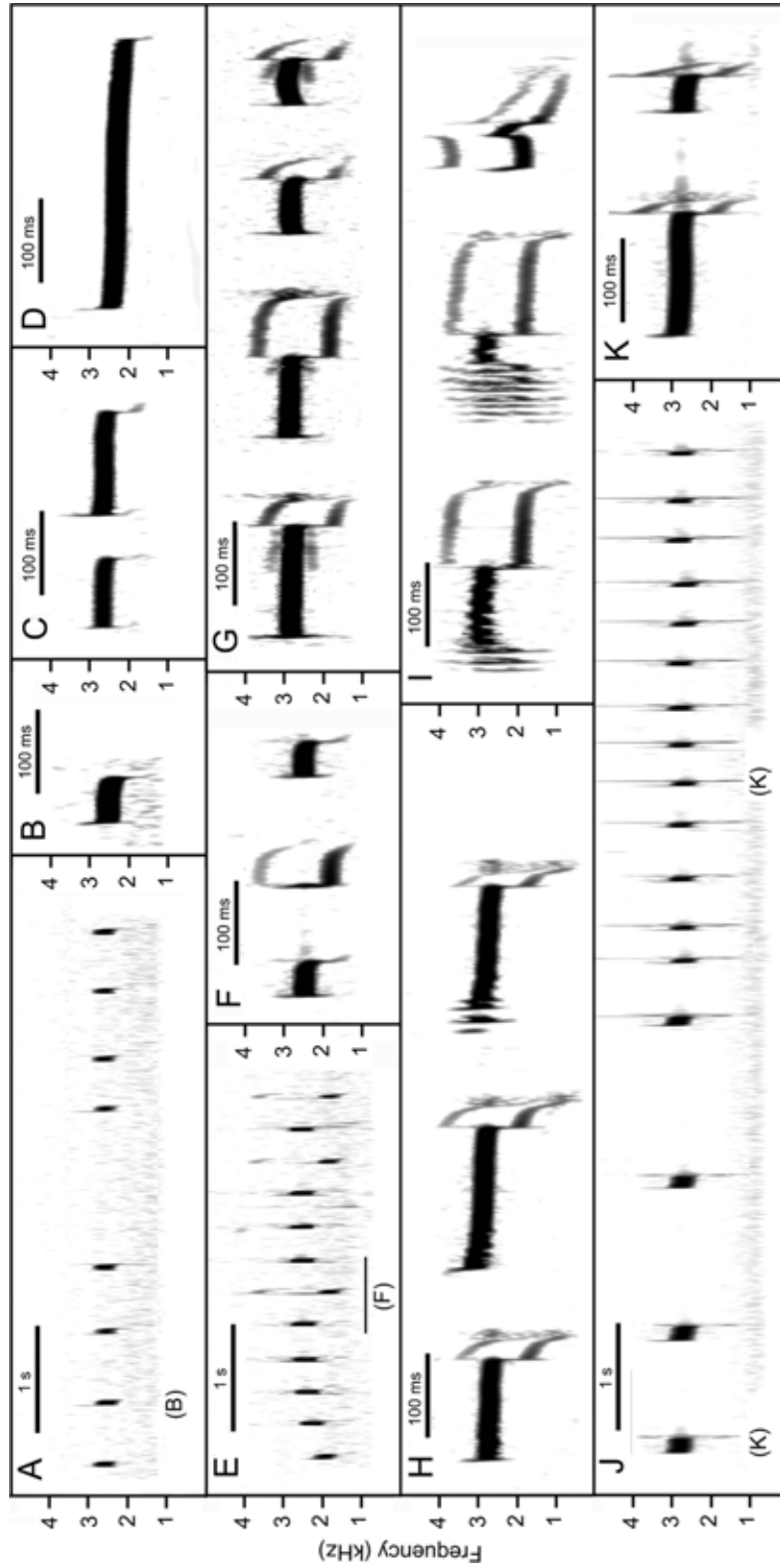
A10 calls were given by parents attending chicks and often were mixed with A11 calls in distraction displays toward predators (including humans). Chicks seemed to respond more strongly to A10 calls than to A9 calls. For example, one attending bird used A10 calls to lead its chick away after the chick did not respond to A9 calls.

A10 calls began and ended abruptly with pulsing and had substantial energy in the second harmonic. Frequency decreased gradually over the call.

#### Adult call type 11 (A11) (Figs. 3G–3K)

As for A9 calls, we used structural and contextual features to assign certain heterogeneous calls to this class. A11 calls were tonal; had no evident harmonics; showed an abrupt frequency decline to a lower-frequency portion with strong

**Fig. 3.** "Piping" (A7 call) and related calls of the piping plover. (A) Portion of long series of A7 calls showing approximately rhythmic temporal pattern; natural intercall intervals are shown (Prince Edward Island). Letter in parentheses indicates call that is analyzed further in panel B. (B) A7 call from panel A, shown as spectrogram on a different timescale. (C, D) Long versions of A7 calls from Prince Edward Island (C) and Saskatchewan (D). (E) Portion of long series of A7 calls showing rapid rhythmic delivery and frequency variation, even between successive calls; natural intercall intervals are shown (Prince Edward Island). Letter in parentheses indicates calls that are analyzed further in panel F. (F) Three A7 calls from panel E, shown as spectrograms on different timescales; arbitrary intercall intervals are shown. (G–I) Selected A11 calls from three different birds (Prince Edward Island; last call in panel I is aberrant). (J) Portion of long series of A11 calls showing variable call duration and temporal pattern; natural intercall intervals are shown (Ontario). Letters in parentheses indicate calls that are analyzed further in panel K. (K) Two A11 calls from panel J, shown as spectrograms on different timescales.





harmonics (sometimes very brief), usually between the middle and end of the call; and were used in the presence of potential predators, including humans.

A11 calls were used by both sexes. With A7 and A12 calls, they were uttered by birds upon the approach of humans, from prenesting through fledging. They were directed toward terrestrial or aerial predators (e.g., herring gulls, *Larus argentatus* Pontoppidan, 1763; American crow, *Corvus brachyrhynchos* Brehm, 1822) near the nest. They also were given during intense distraction displays such as high-tailed running, crouch-running, or injury-feigning. Use of A11 calls peaked in the period of hatching, when aerial calling to distract predators also appeared. High-intensity distraction, with use of this call type plus A13, made the bird conspicuous to predators and led predators from the nest and chicks. Chicks responded to A11 calls by crouching motionless until their parents gave A9 or A12 calls or by moving away from a distracting parent. A11 was one of the most commonly heard call types after hatching. In one exceptional instance, a male used A3, A7, A12, and A13 calls during egg laying, and continued its distraction display until it was 50 m away from its nest.

A11 calls often were given in long, approximately rhythmic series (Fig. 3J). They were of moderately high amplitude and typically featured a long, nonharmonic tonal part with a sharp onset, followed by a part with slowly decreasing frequency, then an abrupt frequency drop to a terminal, declining-frequency part of variable duration and with harmonic structure (Figs. 3G–3I, 3K). As with many other calls of this species, pulsing often occurred just before, just after, or as part of the beginning or end of the call (Figs. 3H, 3I).

Frequency of the first tonal part of the call differed significantly between the sexes: 2.59 Hz in males, 2.73 Hz in females (H.-C.S., unpublished data).

Calls intermediate in structure between A11 and A12, and between A11 and A7, were common (see following section).

This call type was described as *kee-ah kee-ah* by Pickwell (1925).

#### Adult call type 12 (A12) (Fig. 4)

A12 calls were given in diverse contexts. Early in the breeding season, A12 calls were one of three call types (with A7 and A11) given upon human approach. A11, A12, and A13 calls were mixed during distraction behaviour. One male in particular used A12 calls for several minutes toward a common raven resting near the nest on the day of hatching. Secondly, A12 calls were used as contact calls between mates, from parents to chicks, and by parents leading chicks to foraging sites or searching for separated chicks. During the prenesting period, when paired birds flew from their prospective territories, one of the pair often uttered this call type. A12 calls were given by premigratory individuals in small flocks (sometimes in mixed flocks; e.g., with semipalmated sandpiper, *Calidris pusilla* (L., 1766)) and were given frequently by foraging birds that were disturbed by humans; one or two of the birds would utter A12 calls during flight away, then the other birds would follow.

A12 calls may also function to attract females. One lone male gave A12 calls as it passed over another male's territory; the resident male uttered A3 and A7 calls in response. The lone male continued to utter A12 calls as he ap-

proached, landed, and then flew to another location; after landing the second time, he uttered A9 and A12 calls while walking around. On another occasion, a paired female in the prenesting period uttered A12 calls in response to an A12 call given by a lone male flying overhead; the female's mate flew after the other male and drove it away.

A12 calls were uttered at irregular but often brief intervals. They were moderately long and were marked by one to several slowly repeated, deep-frequency dips. As for other call types, pulsing often occurred at the end. The location of peak frequency varied in calls with multiple modulations; amplitude was much weaker at frequency minima than maxima (first calls in Figs. 4A, 4B), and pulsing often occurred at minima (other calls in Fig. 4A, 4B; Fig. 4C). The beginning of A12 calls resembled other call types (e.g., A7, A9, A11; Fig. 4F, first call in Fig. 4G), and calls lacking the frequency dip could be classified as A14 calls (e.g., third call in Fig. 4G).

Frequency differed significantly between the sexes: before frequency dip, 2.25 kHz in males, 2.51 kHz in females; after frequency dip, 1.94 kHz in males, 2.15 kHz in females (H.-C.S., unpublished data).

This call type was described as *peep-lo* by (Cairns 1977) and *woo-up* by Haig (1992).

#### Adult call type 13 (A13) (Figs. 5E, 5F)

During high-intensity distraction, parents near the nest or chicks repeatedly uttered a long, harsh call (brief utterances occurred also). Calls showed variable pulsing, and a second harmonic usually was evident. Pulse rates varied within and across calls: examples in Fig. 11 had a range of ~50–125 Hz.

#### Adult call type 14 (A14) (third call in Figs. 4G, 5B)

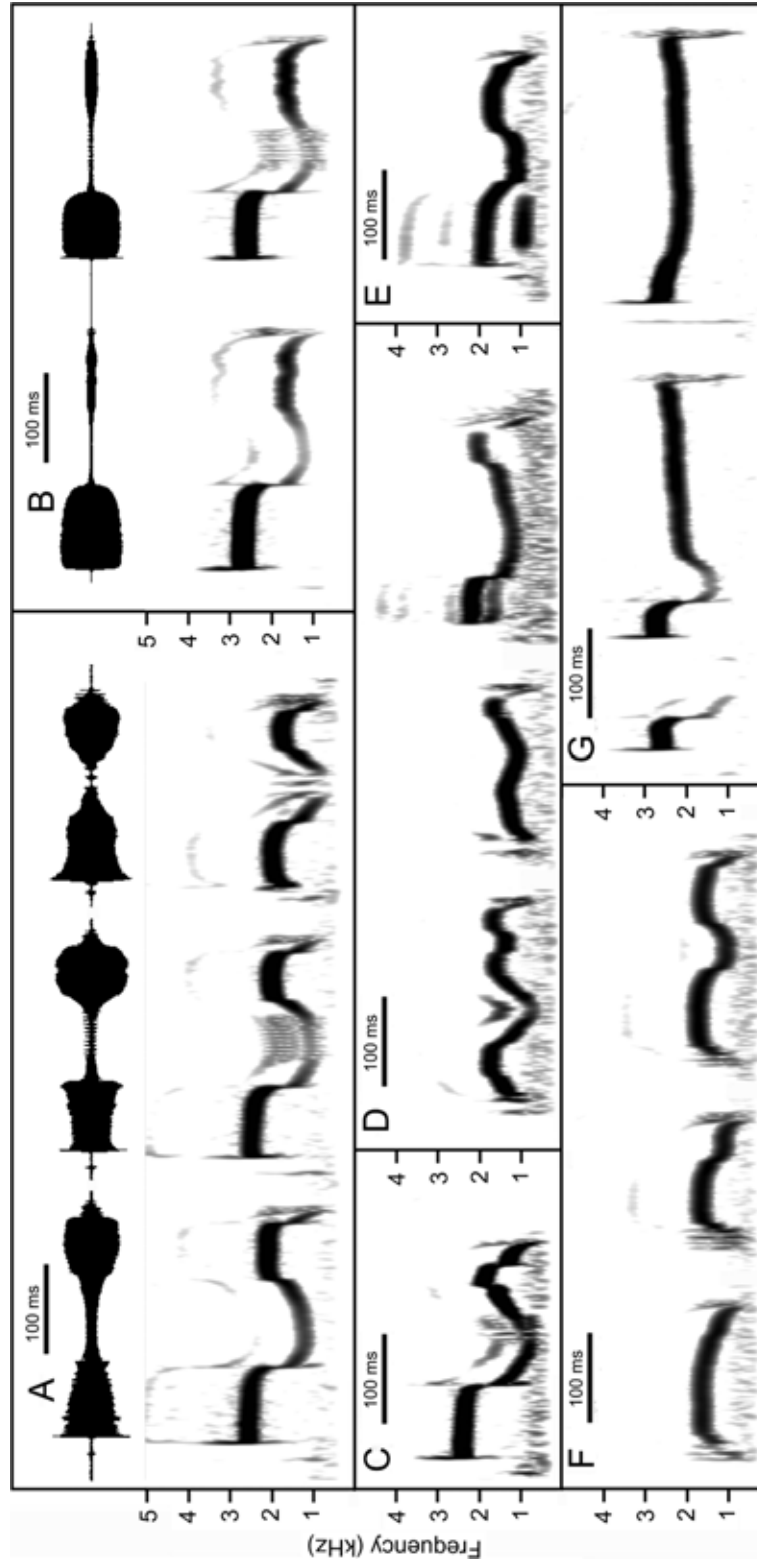
A14 calls were given by adults of both sexes with chicks when aerial predators passed by or suddenly appeared near the chicks. They were common on the day of hatching, when parents were extremely sensitive to and aggressive toward other species. Calling birds often chased low-flying avian intruders, including common raven, herring gull, and common tern (*Sterna hirundo* L., 1758). Some A13 calls in aerial chases resembled A11 or A12 calls.

A14 calls were high in frequency and amplitude, moderately long, and with sudden onset and offset; harmonics were variably evident. Variable patterns of frequency modulation occurred, sometimes as pronounced dips in frequency.

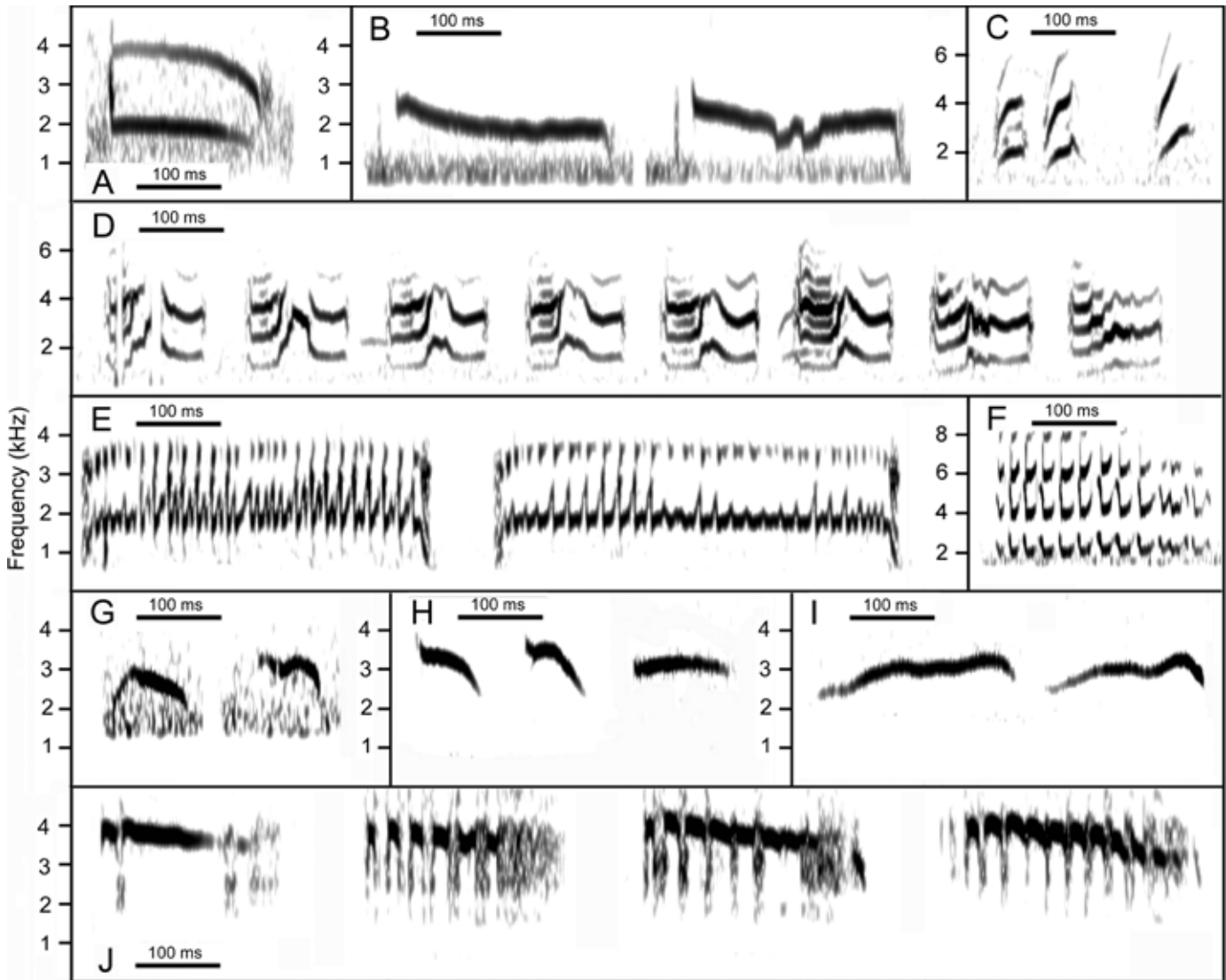
#### Chick call types C1 to C3 (Figs. 5G–5J)

Several types of calls were given by undisturbed chicks with their parents on and after the day of hatching. The calls were given at irregular intervals or approximately rhythmically. C1 calls were given throughout the period of chick care, for example while walking around the nesting or feeding areas; presumably they functioned to maintain contact with siblings or parents. Some variants of this call type were given by a chick apparently seeking its parent after being alone in the foraging area for some time. C2 calls were given when chicks walked near the attending adult on the day of hatching (subsequently it was not possible to record chicks or approach them closely enough to hear this soft call). We could not observe fine details of interactions during

**Fig. 4.** Variation in the "peep-*io*" call (A12) of the piping plover plus examples of structural intergradation among call types. (A) Three A12 calls from a single bird shown as waveforms and spectrograms; arbitrary intercall intervals are shown (Prince Edward Island). (B) Two A12 calls from different birds shown as waveforms and spectrograms; arbitrary intercall interval is shown (Prince Edward Island). (C–E) A12 calls from three different birds; arbitrary intercall intervals are shown in panel D (Prince Edward Island). (F) Structural intergradation between A9 and A12 calls from a single bird; calls are not in sequence (Prince Edward Island). (G) Structural intergradation between A7, A12, and A14 calls (respectively) from a single bird; calls are not in sequence (Prince Edward Island).



**Fig. 5.** Miscellaneous adult calls (concluded) plus chick calls of the piping plover. (A) A10 call (Prince Edward Island). (B) Two A14 calls from a single bird; arbitrary intercall interval is shown (compare rightmost call in Fig. 4G) (Prince Edward Island). (C) Couplet (left) and single (right) A8 calls (couplet with natural intercall interval shown, separated from single call by arbitrary interval) uttered in agonistic interaction between two birds on the ground; note different frequency scale (Saskatchewan). (D) Part of series of A6 calls uttered by one bird in agonistic interaction between two birds on the ground; natural intercall intervals are shown (Saskatchewan). (E) Two A13 calls uttered by a single bird in distraction display near the nest; arbitrary intercall interval is shown (Prince Edward Island). (F) A13 call uttered by a bird in distraction display; note different frequency scale (Ontario). (G, H) C1 calls uttered by chicks at two different nests on day of hatching; arbitrary intercall intervals are shown (Prince Edward Island). (I) C2 calls uttered by chick(s) at nest on day of hatching; arbitrary intercall interval is shown (Prince Edward Island). (J) C3 calls uttered by chick held in hand on day of hatching; arbitrary intercall intervals are shown (Prince Edward Island).



calling, but from audio recordings it was apparent that chicks and parents often counter-called, with adults giving A9, A10, or A12 calls. When we handled chicks for banding, parents stayed nearby and uttered A12 calls.

C1 calls were brief, with variable frequency patterns (Figs. 5G, 5H; Table 2). C1 variants called by one chick seeking its parent were longer and declined in frequency more gradually than typical C1 calls. C2 calls were longer and typically increased gradually in frequency (often with rapid frequency modulation; Fig. 5I).

C1 and C2 calls did not have pulsed parts. C3 calls of chicks held in the hand gradually descended in frequency

and were tonal, and many were segmented as trills with or without broadband noisy sections (Fig. 5J); such calls were harsh-sounding.

## Discussion

### Repertoire size and composition

The term “repertoire” conventionally refers to a species’ set of basic display units and can be applied across multiple structural scales such as song syllables or song types (Kroodsma 1982; Smith 1986, 1991, 1996, 1997; Bain 1992). At the level of call type, we recognize 14 categories

**Table 2.** Summary of descriptive statistics for measured variables<sup>a</sup> of vocalizations of piping plover chicks recorded in Prince Edward Island National Park, 1998–1999.

Call types and variables ( <i>n</i> = no. of calls)	Grand mean ± SD (range)
<b>C1</b> ( <i>n</i> = 53; recordings from five nests)	
Duration, total	79±21 (39–147)
Dominant F <sup>b</sup>	3121±222 (2390–3484)
<b>C2</b> ( <i>n</i> = 23; recordings from five nests)	
Duration, total	361±120 (86–489)
Dominant F	3067±236 (2643–3535)
<b>C3</b> ( <i>n</i> = 23; recordings from three chicks <sup>c</sup> )	
Duration, total	261±55 (135–327)
Dominant F	3662±226 (3198–3939)

<sup>a</sup>Units are ms or Hz, as appropriate.

<sup>b</sup>F, frequency.

<sup>c</sup>Grand mean ± SD refers to *n* = 3 birds for this sample; range refers to total calls.

for adult piping plovers and three for newly hatched chicks. These estimates are conservative because (i) they exclude nonbreeding vocalizations and developmental changes, (ii) some call types could be divided more finely (e.g., A9, A11, C1, C2), and (iii) some call types were undersampled (notably short-distance calls between mates, during agonistic encounters, and between parent and offspring during the brood-rearing period; Snowdon 1986). The repertoire of call types of this species therefore must be >17 but still seems likely to fall within the range (mainly 15–35) for most species (Moynihan 1970).

Vocalizations of piping plovers are diverse. Individual calls (including those repeated within series, such as A4) of adults range from ~10 ms (brief A9 calls) to nearly 1.5 s (long A3 calls) in duration — about two orders of magnitude. Frequencies also span a substantial range, with peak frequency of the first harmonic in adult calls ranging from <900 to >3000 Hz (the range would be much greater using maximal or minimal frequency as a measure). Frequency bandwidth ranges from narrow (e.g., A3, C1, and C2) to broad because of frequency shifts (e.g., A11, A12), broadband pulsing (e.g., A4, C3), or harmonics (e.g., A6, A13, and many A11 calls). Some call types are harsh-sounding owing to broadband pulsing (e.g., adult distraction calls, A13; chicks held in the hand, C3). Other contrasts are apparent, as in short versus long calls (e.g., A3 vs. A9); smoothly rising versus smoothly declining frequency (e.g., A3 vs. A11); and flat versus changing frequency (e.g., some long A11 vs. A3, A10, and A12).

Individual attributes of piping plover vocalizations are simple and few in number but combine to form complex calls having tonal sections with variable harmonic strength; sharp onsets, terminations, or transitions in frequency; pulsing; etc. A striking feature of the species' repertoire is the occurrence of the same attributes in different call types (e.g., introductory or pulsing; sharp frequency transitions), with the attributes being organized similarly across call types. A good example of this is A1 and A4 calls: the latter resemble a highly abbreviated and rapidly repeated version of the former (Figs. 1A–1D). Other call types share features that oc-

cur in similar positions in calls; e.g., introductory and terminal pulsing occurs in many call types. In summary, (i) diverse call types in this species result from recombination of and quantitative variation in acoustic attributes, and (ii) the repertoire is marked by shared attributes and organization of attributes across call types.

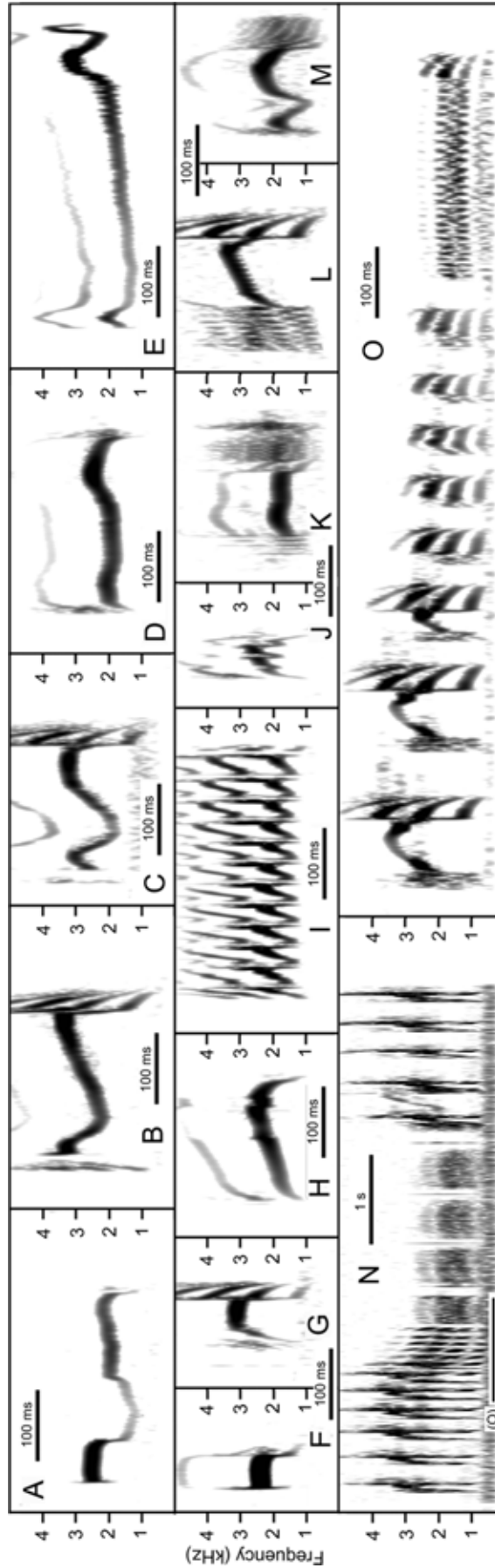
The term “syntax” can refer loosely to nonrandom patterns of association or sequencing of acoustic properties or elements, within or across call types (Hailman et al. 1985; Miller and Murray 1995). The nonrandom positioning (within and across call types) of features such as pulsing (usually at a call's beginning or end) can be considered a form of within-call syntax. Similarly, different call types begin (or end) with a sharp onset to a weakly harmonic tonal section of variable duration, which declines slightly and progressively in frequency (e.g., A7, A11, A12, and some A9 calls). Within-call syntax is expressed also as temporal patterns (e.g., rhythmicity within A1 and A4; bouting and rhythmicity of A2, A4, and A5 calls; drift across A4 call units in duration, pulsing, rate of calling; Smith 1986, 1991, 1996, 1997). At a higher level of organization, syntax is apparent in the common association of A1a, A3, and A4 calls in sequences such as A1a-A3, A1a-A4, and A3-A4 and of A1b and A2 calls in long ground-calling sequences (A1b-A2-A1b-A2, etc.). Such high-level syntactical arrangements increase the species' vocal diversity beyond the level of the basic call types that constitute the repertoire.

We did not investigate call function in this study, but our observations suggest that multiple functions and meanings characterize the communication system; hence, vocal communication is heavily context-dependent (Smith 1977, 1997). For example, different and diverse call types occur in the presence of potential predators (Simmons 1955; Gochfeld 1984), and piping plovers and other shorebird species vocalize extensively outside the breeding period, e.g., during migration and migratory stopovers and on wintering grounds (Recher and Recher 1969; Myers 1984; Piersma et al. 1991; Chojnacki and Kalejta-Summers 1999; Tulp and Koutný 1999). Nonbreeding piping plovers exhibit much agonistic behaviour that includes vocalizations even in midwinter, both intra- and inter-specifically, and in response to potential predators (Johnson 1987; E.H.M., unpublished data). Vocalizations of wintering piping plovers include piping (A7 and brief A11 calls) in response to human approach (E.H.M., unpublished data). Therefore, to determine call functions, a broad approach that includes year-round samples and addresses both signal and extra-signal (contextual) sources of information would be appropriate.

### Acoustic homologies in Charadriidae

Our study is the most detailed account of vocalizations of any plover species to date. Some comparisons and generalizations are possible, however. General features of acoustic structure and organization in piping plovers occur widely throughout Charadriidae, but some extremes in piping plovers are surpassed by those in other species. Thus, *tic* calls uttered by double-banded plovers (*Charadrius bicinctus* Jardine and Selby, 1827) in BFs are briefer than any calls of *C. melodus* and are uttered at higher rates (Phillips 1980; Marchant and Higgins 1993), and vocalizations of adult *C. vociferus* (paradoxically, a larger species) reach much

**Fig. 6.** Acoustic homologies in Charadriidae span multiple structural levels. (A) A12 (“peep-lo”) call of piping plover (*Charadrius melodus*; Saskatchewan) and presumed homologues in (B, C) semipalmated plover (*C. semipalmatus*; British Columbia and Nunavut, respectively); (D) common ringed plover (*C. hiaticula*; Russia); and (E) western snowy plover (*C. alexandrinus nivosus*; Oregon). (F) A7 (“piping”) or A11 call of *C. melodus* (Saskatchewan) from long rhythmic call series and presumed homologues (also from long rhythmic call series) in (G) *C. semipalmatus* (Nunavut) and (H) *C. hiaticula* (Russia). (I, J) Calls of (I) western snowy (Oregon) and (J) Peruvian (*C. alexandrinus occidentalis*; Peru) plovers, exhibiting extremes in duration (numerous calls of intermediate duration in the latter subspecies are in MLNS 23961); these may represent ritualized rapid delivery of individual piping elements. (K) A1a call (call in butterfly flight) of *C. melodus* (Saskatchewan) and presumed homologues in (L) *C. semipalmatus* (Nunavut) and (M) *C. hiaticula* (Russia). (N) Presumed homologue of A1a-A4-A3 vocal sequence in *C. semipalmatus* (Nunavut; see Fig. 1; timescale of this panel corresponds to that of Fig. 1A) (natural intercall intervals are shown). The bird was calling on the ground, repeatedly uttering A4-A3 sequences within a long A1A sequence, but this is a very common vocal form during butterfly flights throughout the species’ range (E.H.M., unpublished data). Letter in parentheses indicates section that is analyzed further in panel O. (O) Abbreviated A1a calls merging into A4 sequence and first of four A3 calls.



higher fundamental frequencies (>8 kHz; Borror 1970; Bursian 1971; Phillips 1972; Nol 1980; Cramp 1983; Gaunt 1983; Jackson and Jackson 2002).

Trills (series of rapidly repeated, brief calls of similar structure) are common in birds but poorly represented in the repertoire of piping plovers (A5, A13, and many C3 calls); however, they occur in many other charadriines including *C. alexandrinus* (Figs. 6I, 6J), greater sandplover (*Charadrius leschenaultii* Lesson, 1826), lesser sandplover (*Charadrius mongolus* Pallas, 1776), mountain plover (*Charadrius montanus* Townsend, 1837), Eurasian dotterel (*Charadrius morinellus* L., 1758), red-capped plover (*Charadrius ruficapillus* Temminck, 1822), Oriental plover (*Charadrius veredus* Gould, 1848), and *C. vociferus* (Bursian 1971; Graul 1974; Glutz et al. 1975; Nol 1980; Bergmann and Helb 1982; Cramp 1983; Maclean 1985; Gebauer and Nadler 1992; Marchant and Higgins 1993).

Sudden frequency shifts with concomitant changes in harmonic richness, as in many A11 calls of piping plovers, appear to be uncommon in other charadriines: only published spectrograms for little ringed plovers (*Charadrius dubius* Scopoli, 1786) show this feature (Glutz et al. 1975; Bergmann and Helb 1982; Cramp 1983). Such shifts are striking in the genus *Pluvialis*, however (Greenewalt 1968; Tikhonov and Fokin 1981; Bergmann and Helb 1982; Cramp 1983; Miller 1984, 1996; Maclean 1985; Nethersole-Thompson and Nethersole-Thompson 1986; Richard 1991; Connors et al. 1993; Johnson and Connors 1996; Byrkjedal and Thompson 1998). Curiously, this sort of shift may be absent from *Vanellus*, despite this genus apparently having the most complex vocalizations in the family (Dabelsteen 1978; Cramp 1983; Miller 1984; Maclean 1985; Nethersole-Thompson and Nethersole-Thompson 1986; Robisson 1987; Ward 1987, 1989; Ward and Maclean 1988; Walters 1990).

We observed no nonvocal sounds in piping plovers. Male *C. bicinctus* produce a loud clicking sound with each wing-beat during BFs (Bamford 1986; Marchant and Higgins 1993), and wing-generated sounds are produced during display flights of male northern lapwings (*Vanellus vanellus* (L., 1758)) (Glutz et al. 1975; Dabelsteen 1978; Cramp 1983).

Structural features of vocalizations, combined with contextual or behavioural information, may permit inference of homology on different scales, from fine-scale call features to call types, etc. (Miller 1996). Inference often is possible even for structurally simple calls that occur in readily characterized circumstances, because of the small interpretive differences among observers. Distraction displays provide one example: vocalizations given by distracting parents vary in duration across species but are uniformly repeated and harsh-sounding (pulsed or broadband, or both) in *C. alexandrinus*, *C. melodus*, *C. mongolus*, *C. montanus*, *C. semipalmatus*, and Wilson's plover (*Charadrius wilsonia* Ord, 1814) (Graul 1974; Cramp 1983; Bergstrom 1988; Gebauer and Nadler 1992; Nol and Blanken 1999). Spontaneous vocalizations by chicks of *C. dubius* and *C. hiaticula* before hatching or early in life are similar to those we analyzed

(Tikhonov and Fokin 1979, 1980), and vocalizations uttered by young chicks held in the hand are very similar in *C. melodus*, *C. montanus*, and *C. vociferus* (Heckenlively 1972; Graul 1974).

A less well-defined context is when adult breeding plovers vocalize upon being approached by a human (pairing or breeding status of birds often is unknown; the bird may be calling to its mate or chicks, etc.). Piping plovers utter many A7, A11, and A12 calls in such a situation. Based on context and structure (moderately brief tonal calls with distinctive inflections, uttered singly), the homologue to A12 of *C. melodus* seems to be widespread in related species: *quoit* of wrybill (*Anarhynchus frontalis* Quoy and Gaimard, 1830)<sup>3</sup>; *turwheet* (*towheet*) of *C. alexandrinus* (Fig. 6E); *whee-o-whit* of *C. bicinctus*; "general contact and alarm note" of *C. hiaticula* (Fig. 6D); *tu-lup* of *C. montanus*; *poo-eeet* of *C. ruficapillus*; and "common call note" of *C. semipalmatus* (Figs. 6B, 6C) (Graul 1974; Phillips 1980; Cramp 1983; Marchant and Higgins 1993; Page et al. 1995; Nol and Blanken 1999). A second call type often is uttered by adult birds in the same circumstances, but relationships to A7 and A11 calls are unclear. In most species the calls are tonal and resemble those of *C. melodus*, as in *A. frontalis*, *C. bicinctus*, *C. dubius*, *C. hiaticula* (Fig. 6H), *C. mongolus* (?), *C. morinellus*, *C. wilsonia*, and New Zealand shore plover (*Charadrius novaeseelandiae* Gmelin, 1789) (Glutz et al. 1975; Phillips 1977, 1980; Bergmann and Helb 1982; Cramp 1983; Bergstrom 1988; Gebauer and Nadler 1992; Marchant and Higgins 1993; Corbat and Bergstrom 2000). In contrast, the other call form used by red-breasted plovers (*Charadrius obscurus* Gmelin, 1789) and *C. alexandrinus* (Figs. 6I, 6J) is a rapid, brief trill (Glutz et al. 1975; Phillips 1980; Bergmann and Helb 1982; Cramp 1983) that may represent a formalized fusion of individual elements. In *C. semipalmatus* the call has pronounced introductory and terminal pulsing, thus resembling the species' A12 call (Fig. 6G).

Complex vocalizations and vocal sequences used in mate attraction, territorial advertisement, agonistic displays, etc., may diverge rapidly between related species. In plovers, widespread display forms are repeated vocalizations during BFs (A1a calls of piping plovers) and other complex vocalizations (A3, A4). BFs occur in most species and populations of charadriids but are lacking in some, such as *C. a. nivosus* and *C. obscurus* (Phillips 1980; Warriner et al. 1986). Homologues to A1a calls seem readily identifiable for *C. alexandrinus*, *C. bicinctus*, *C. dubius*, *C. hiaticula* (Fig. 6M), *C. montanus*, *C. semipalmatus* (Fig. 6L), and black-fronted dotterel, *Elseya melanops* (Vieillot, 1818) (Glutz et al. 1975; Phillips 1980; Bergmann and Helb 1982; Cramp 1983; Krey 1991; Marchant and Higgins 1993; Miller 1996)<sup>4</sup>. Calls begin and end with pulsed parts in most species, and pulsing is differentiated (e.g., introductory pulsing is fast and terminal pulsing is slow in calls of *C. hiaticula* and *C. semipalmatus*; Miller 1996). Tonal call parts differ among species in duration and particularly in the nature of modulations. Introductory and terminal pulsing asso-

<sup>3</sup>Phillips (1980, p. 190) stated that he "heard nothing resembling this ... call", but his spectrograms and descriptions suggest to us that the *quoit* call of *Anarhynchus* may be homologous.

<sup>4</sup>Some spectrograms attributed to Kentish plover in Glutz et al. (1975) and Bergmann and Helb (1982) are incorrect: they depict vocalizations of dunlin (*Calidris alpina* (L., 1758); Krey 1991).

ciated with rhythmically repeated calls during flight displays may be highly conserved evolutionarily, as they occur also in some *Pluvialis* species (Connors et al. 1993; Miller 1996; Byrkjedal and Thompson 1998).

Other complex vocalizations occur in charadriines. When they are treated in isolation as different call types, they are difficult to homologize, but some patterns emerge upon considering associative or sequential relationships and contexts of use. Call types A3 and A4 of piping plovers can serve this point. The structurally distinctive A3 call invariably was uttered in brief rhythmic sequences and frequently was associated with (i.e., followed) A4 calls, in BFs or on the ground. Structurally similar call types have been described for *C. bicinctus* (“a mooing or moaning call”; Phillips 1980, p. 181) and *C. montanus* (Graul 1974). Are these homologous with A3 calls of *C. melodus*? Evidence for homology could come from association with other call types (Miller 1996), as for *C. semipalmatus*, in which (as in piping plovers) rhythmic A1a calling in BFs is interrupted or followed by calls that strongly resemble the sequence A4-A3 of *C. melodus* (Figs. 6N, 6O). In both species, the calls are uttered commonly in agonistic interactions, chases, etc. Harsh-sounding call sequences have been described for many species, and we suggest that homologues to A4 include (*wee-chedle* of *C. bicinctus*, “song rattle” of *C. mongolus* and *C. wilsonia*, “churr” of *C. obscurus*, and “rattle” of *C. novaeseelandiae* (Phillips 1977; Bergstrom 1988; Gebauer and Nadler 1992; Marchant and Higgins 1993; Knopf 1996; Corbat and Bergstrom 2000).

Vocalizations of Charadriidae share many features, and some call types are readily homologized based on acoustic structure and contextual use. Such apparent evolutionary conservatism, both in specific attributes and syntax, suggests that the family offers opportunities for investigating patterns in and constraints on evolution of vocalizations. Intriguingly, plover vocalizations may prove to be phylogenetically informative over a range of levels, because some calls differ greatly even between putative subspecies; for example, upon being flushed, wintering *Charadrius dubius curonicus* in New Guinea utter a “softly whistled *pee u*” (resembling the “peep-lo” of piping plovers and other species; Fig. 6), in contrast to the *chit chit chit* of the resident nonmigratory *Charadrius dubius dubius* (Carter and Rogers 1998, p. 272).

## Acknowledgements

We thank staff and volunteers of Parks Canada (PEINP) and Environment Canada (Canadian Wildlife Service) for advice, encouragement, assistance, and moral support in planning and conducting field work: D. Amirault, P. Ayles, E. Clow, S. Gagnon-Provencher, P. Goossen, K. Kinnear, L. LaFosse, B. LeFresne, P. McCabe, P. McIntyre, J.-E. Proud, L. Thomas, and S. Westworth; C. Barnes and J. Watson provided essential assistance with equipment and supplies. The staff of the Macaulay Library of Natural Sounds, Cornell University, were extremely helpful on many occasions. Funding was provided by Canadian Wildlife Service, Memorial University, Natural Sciences and Engineering Research Council of Canada (Discovery Grant to E.H.M.), and PEINP.

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