

VOCAL COMMUNICATION AND INDIVIDUALITY OF
PIPING PLOVERS (*CHARADRIUS MELODUS*):
DESCRIPTION, QUANTIFICATION, AND APPLICATIONS
FOR MANAGEMENT

CENTRE FOR NEWFOUNDLAND STUDIES

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**VOCAL COMMUNICATION AND INDIVIDUALITY OF PIPING PLOVERS
(*CHARADRIUS MELODUS*): DESCRIPTION, QUANTIFICATION, AND
APPLICATIONS FOR MANAGEMENT**

by

Ha-Cheol Sung

A thesis submitted to the
School of Graduate Studies
in partial fulfilment of the
requirements for the degree of
Master of Science

Biopsychology Programme
Memorial University of Newfoundland

December, 1999

St. John's

Newfoundland

ABSTRACT

Vocalizations of Piping Plover (*Charadrius melodus*) were studied in Prince Edward Island National Park during the breeding seasons of 1998 and 1999, and in Cheeseman Provincial Park in Newfoundland in May 1999 (early breeding season). Ten distinct call types of adults and three types of chicks were identified. Behavioural contexts of call-use are described and interpreted.

The size of the vocal repertoire of the Piping Plover was similar with that of other *Charadrius* species. Five call types appeared to function as alarm signals, which thus occupied a major functional category of communication in this species. Vocal signals and functional characteristics in this and other *Charadrius* species show structural properties consistent with adaptation to open-country environments: low frequency, frequency-modulated tones, and redundancy via signal repetition. Brief, short one- or two-note calls were extensively used as a contact call between mates or from parent to chicks over short distances. Alarm calls were characterized by locatable properties including increasing and decreasing frequency. Piping Plovers emitted 'chatter' and 'whistle' calls in relationship to high- and low-level alarm, respectively. All call types except one were uttered by both male and female. The exception (call type I) was used predominantly by newly arrived males in aerial displays, and may serve for attracting females, defending territory, and stimulating mating.

Sexual and individual variation were investigated in four of ten call types of adults. Classification trees, a statistical technique to partition calls into homogeneous sets, were constructed for identifying individuals.

Visual assessment of calls was applied only to call type I of males; nine males differed greatly from one another and their calls were stable between two sample periods. Results of statistical analysis on call type I also revealed significant differences among males, and some significant differences between periods. Quantitative analysis of call types VI and VIII showed significant differences among individuals and between sexes, and differed on some variables between two periods. However, classification tree of male constructed with call type I and combined call types VI and VIII for male and call types VI and VIII for female identified individuals with very little misclassification rate. One male banded in 1998 and recorded in 1998 and 1999 was successfully identified using one of the trees. Possible reasons for variation within individuals and usefulness of the technique are discussed.

ACKNOWLEDGMENTS

I am very grateful to my advisor, Edward H. Miller, for his invaluable guidance, support, and encouragement throughout this study. I feel fortunate to have had an opportunity to work with an advisor who showed excellent professionalism and mentoring lab students. I would also like to thank committee members Dr. Ian Jones and Dr. John Green for their many helpful comments and warm attention. I would especially like to thank to Dr. Stephen Flemming for his invaluable guidance in providing information on Piping Plovers.

I sincerely thank the staff of the Canadian Wildlife Service, PEI National Park, and Cheeseman Provincial Park for their cooperation, assistance, and kindness: Diane Amirault, Philip McCabe, Linda Thomas, Katrina Kinnear, Jami-ellen Proud, Peter McIntyre, Erin Clow, Paul Ayles, Bill LeFrense, and Lorna LaFosse. It will be unforgettable memories to have shared the experience on the small cute shorebird.

I wish to extend great appreciation to Dr. Anne Storey and Dr. William Montevocchi for their warm attention and to Mark Hipfner, Jackie Weir, Morley and Nami Choi for their friendship during graduate school. I am also thankful to past and present lab friends, Valerie Moulton, Arturo Serrano, Rebecca Jeffery, Lauren Burton, Cliff Guy, Shumona Saha, Linda Hoang, and Mary Ann St John. Finally, I thank my family for their endless love and concerns from the start to the end of graduate school.

Funding was provided by the Canadian Wildlife Service, PEI National Park, and the Biopsychology programme and Biology Department at Memorial University of Newfoundland.

TABLE OF CONTENTS

	Pages
Abstract.....	ii
Acknowledgements.....	iv
Table of Contents.....	v
List of Tables.....	vii
List of Figures.....	ix
Chapter 1: Introduction.....	1
Chapter 2: Vocalizations of Piping Plover	
Introduction.....	4
Methods.....	7
Results.....	13
Adult vocalizations.....	13
Chick vocalizations.....	26
Discussion.....	30
The size of repertoire.....	30
Adaptation of vocal signals to open habitats.....	34
Vocalizations and pair formation.....	39
Chapter 3: Individual and sexual differences in vocalizations of Piping Plovers	
Introduction.....	41
Methods.....	43
Study area and recordings.....	43

	Pages
Data analysis.....	45
Results.....	49
Individuality in call type.....	49
Vocal differences among individuals.....	49
Vocal differences of call type I between the two periods.....	49
Vocal differences of call type I between aerial and ground calls.....	55
Individuality in call types VI, VII, VIII.....	55
Sexual differences.....	55
Individual differences.....	55
Variation of call types VI, VII, and VIII between breeding stages...	60
Classification tree analysis.....	65
Discussion.....	78
Individual variations in call type I.....	78
Individual variations in call type VI, VII, and VIII.....	79
The use of Piping Plover vocalizations as a census tool.....	81
Chapter 4: Conclusions.....	83
References.....	86
Appendix A: Summary of information on the study animals.....	97
Appendix B: Quantitative analysis of call type VI of Piping Plovers.....	100
Appendix C: Quantitative analysis of call type VII of Piping Plovers.....	103
Appendix D: Quantitative analysis of call type VIII of Piping Plovers.....	106

LIST OF TABLES

Table 2.1	Synopsis of adult Piping Plover vocalizations.....	14
Table 2.2	Quantitative treatment of call types of adult Piping Plovers.....	15
Table 2.3	Quantitative treatment of call types of chick Piping Plovers.....	28
Table 2.4	Comparison of the number of vocal signals in adults of selected species of birds.....	31
Table 2.5	Comparison of structure and function of vocalizations in adults of <i>Charadrius</i> species.....	35
Table 3.1	Summary of means and coefficients of variation (CV) of Call type I among nine males Piping Plovers in 1998.....	52
Table 3.2	Summary of CV - ratios and results of one-way ANOVAs with multiple comparisons for call type I.....	53
Table 3.3	Summary of data, and results of one-way ANOVAs for comparisons of call type I between two periods for two males.....	54
Table 3.4	Summary of autocorrelation analysis for call type I within the same male on two dates.....	56
Table 3.5	Summary of data, and one-way ANOVAs comparing type I calls given in the ground and in the air.....	57
Table 3.6	Results of nested analyses of variance on F-variables variable (calls within individuals within sex)	58
Table 3.7	Summary of data on variation in selected calls at individual and population levels.....	59
Table 3.8	Results of autocorrelation of call type VIII.....	62
Table 3.9	Mean \pm SD, and results of Mann-Whitney tests comparing vocal variables of call types VI in 1998.....	63
Table 3.10	Mean \pm SD, and results of Mann-Whitney tests comparing vocal variables of call types VIII in 1998.....	64

Table 3.11	Summary of mean \pm SD showing variations of calls from the same individuals between breeding stages in 1998.....	66
Table 3.12	Summary of results from three different classification trees on both sexes.....	76
Table 3.13	Comparisons of the calls of banded males in 1998 and banded male that returned in 1999.....	77

LIST OF FIGURES

Figure 2.1	Piping Plover study areas (in black) within PEINP.....	8
Figure 2.2	Breeding schedule of the Piping Plover at PEINP.....	9
Figure 2.3	Examples of variables used in the study.....	11
Figure 2.4	Sonagrams of Piping Plover vocalizations (part 1/4)	16
Figure 2.5	Sonagrams of Piping Plover vocalizations (part 2/4)	21
Figure 2.6	Sonagrams of Piping Plover vocalizations (part 3/4)	24
Figure 2.7	Sonagrams of Piping Plover vocalizations of chicks (part 4/4)	27
Figure 3.1	Examples of variables used in the study.....	46
Figure 3.2	Sonagrams of call type I showing differences among individuals...	50
Figure 3.3	Sonagrams of call type I recorded within the same territory of different periods.....	51
Figure 3.4	Sonagrams of call type VI recorded in 1998 showing differences between individuals.....	61
Figure 3.5	Classification tree of call type I recorded in 1998 to predict males from call variables.....	67
Figure 3.6	Boxplots of call type I variables showing data distributions for each individual.....	68
Figure 3.7	Classification tree of call types VI, VIII from females recorded in 1998 to classify individuals from the call variables.....	71
Figure 3.8	Boxplots of call type VI, VIII variables of females.....	72

Figure 3.9	Classification tree of call types VI, VIII from males recorded in 1998 to classify individuals from the call variables.....	73
Figure 3.10	Boxplots of call type VI variables showing the data distribution of males.....	74

CHAPTER 1. INTRODUCTION

Communication is a process of information exchange between sender and receiver. Senders make information available through signals, and receivers interpret information using the signals, other stimuli, experience, etc. (Smith 1990). Receivers are expected to be highly sensitive to senders' signals, and senders transmit and modify signals to manipulate receivers to the benefit of the senders (Johnstone 1997). Conspicuous and stereotyped vocal signals provide many obvious benefits. For instance, the vocal patterns peculiar to one's own species are important for species recognition. Vocalizations that differ between the sexes play important roles in mate choice and male-male or female-female competition, and can reduce costs (e.g. cost time) from ambiguity.

Many avian species also show vocal individuality and can discriminate between pair members, relatives, or neighbours (Wanker et al. 1998; Wiley and Wiley 1977; Colgan 1983; Beecher 1988, 1989; Ydenberg et al. 1988; Studholme 1994). Individuality can be determined by visual inspection of sonagrams or by quantitative analyses. The latter are particularly important for identifying individuals as a census tool (Beightol and Samuel 1973; McGregor and Byle 1992; Peake et al. 1998). Beightol and Samuel (1973) and Galeotti et al. (1993) used multiple variables for identifying individuals, and Peake et al (1998) re-identified individuals with an improved technique by adding information on fine temporal structure to the discriminant function analysis of Corn Crake calls. However, Eakle et al. (1989) failed to identify individuals because of high intraindividual variation. Vocal signals have many advantages for endangered or threatened species

because they can be recorded with minimal disturbance in comparison with capturing and marking efforts. Furthermore, vocal analysis is useful for nocturnal or shy species.

The Piping Plover (*Charadrius melodus*) is an endangered species of shorebird that breeds on wide sandy beaches of the Great Lakes, on the northern Great Plains of Canada and the United States, and along Atlantic coastal areas. Predation and habitat loss from human activities greatly influence breeding success (Flemming et al. 1988; Prindiville Gaines and Ryan 1988). The species is socially monogamous, and shows sexual differences in fine features of bill and plumage; males have darker and more complete forehead and breast bands, and orange bills than females (Haig 1992). Both pair members defend their territory throughout the breeding season. Most egg-laying occurs from the end of April to mid-May, and incubation averages 28 days (Cairns 1977; Thomas et al. 1998, 1999). Both pair members incubate the eggs and attend chicks after hatching. Fledging takes place at > 26 days of age in Nova Scotia (Cairns 1977).

The Piping Plover has been listed as an endangered species in Canada since 1985 and as a threatened and endangered species in the U. S. A. since 1986, so intensive conservation efforts to restore populations have been promoted (Haig 1992). As one effort for management and conservation, vocalizations may be used to monitor population trends and size. Therefore, the main goal of the first part of this study (Chapter 2) was to examine the structure and variation of vocalizations, together with the functions they convey. Accurate understanding of associated behaviour and functions for different call types will improve understanding and promote standardization of field observations. The second part (Chapter 3) characterizes individual and sexual variation

in selected vocalizations, and evaluates the potential of vocalizations as a census tool.

CHAPTER 2. VOCALIZATIONS OF PIPING PLOVER

INTRODUCTION

In the process of avian communication, vocal signals play an important role in expressing a signaler's identity, sex, motivational state, and reproductive status (Marler 1956, 1977; Smith 1977). Vocal repertoires of birds are adapted to their social systems as well as to their habitats (Sordahl 1979; Johns et al. 1989; Trainer and McDonald 1993). Many studies have detailed acoustic structure and vocal functions (Oring 1968; Ficken et al. 1978 ; Anderson 1978; Maier 1982; Riska 1986; Anjos and Vielliard 1993; Byers 1996). Such research typically relies on sonagrams and oscillograms for revealing acoustic structure, and has contributed to improve theoretical frameworks for understanding vocal communication.

The approach of message-meaning analysis by Smith (1977) emphasized the significance in communication of contextual information that lies outside the physical signal itself; receivers use the signal plus contextual information in selecting a response. This approach involves description of signals and their variants, and correlating their occurrence with contextual features. In some cases, the "meaning" of a signal to a receiver can be inferred by noting the receiver's response to the signal, though there are problems with this technique (Smith 1977).

Many shorebirds inhabit open environments and show adaptive structural properties in vocal signals and temporal patterning of signals (Sordahl 1979; Miller 1984; 1996). Birds inhabiting open environments must communicate in the face of much background

noise, such as sounds of wind and waves, and must do so over long distances. Some widespread adaptations are to use signals of low frequency to reduce attenuation rate, to use unmodulated sounds, and to use narrow- rather than broad band sounds that soon become undetectable in noisy environments (Morton 1975; Wiley and Richards 1982; Brown and Handford 1996). Many shorebirds also perform aerial displays to increase transmission distance and conspicuousness.

Vocalizations of Piping Plovers have been described by several authors, but only two sonograms (aerial courtship and nest-scraping calls) have been published (Haig 1992). The lack of adequate description is an impediment to many management initiatives (e.g. in unambiguous observational protocols) and also makes comparison with other members of the Charadriidae impossible. To date, vocalizations of Charadriidae have been well-described only for the following species: Killdeer (*C. vociferus*; Phillips 1972), Mountain Plover (*C. montanus*; Graul 1974), New Zealand Plovers (Phillips 1980), Little Ringed Plover (*C. dubius*; Cramp et al. 1983), Ringed Plover (*C. hiaticula*; Cramp et al. 1983), Wilson's Plover (*C. wilsonia*; Bergstrom 1988), and Lesser Sand Plover (*C. mongolus*; Gebauer and Nadler 1992).

The main goal of this part of the study was to describe vocalizations, and to infer social functions of vocalizations. Specific objectives include:

- (1) to analyze and describe vocal signals sonographically
- (2) to describe the behavioural contexts of the vocal signals and infer probable functions

- (3) to provide a detailed baseline of the vocal repertoire for future studies
- (4) to interpret the adaptive significance of vocal signals in open habitats
- (5) to compare this species' vocalizations with other *Charadrius* species

METHODS

Research was conducted in Prince Edward Island National Park (PEINP) from 1 May to 30 July 1998 and 17 May to 15 July 1999, and in Cheeseman Provincial Park, Newfoundland, from 1 to 15 May 1999 (Figs. 2. 1, 2. 2). PEINP was divided into four study areas (Fig. 2. 1): Cavendish ($46^{\circ}30' \text{ N}$, $63^{\circ}25' \text{ W}$), Brackley Beach ($46^{\circ}25' \text{ N}$, $63^{\circ}13' \text{ W}$), Blooming Point ($46^{\circ}24' \text{ N}$, $62^{\circ}59' \text{ W}$), and Greenwich ($46^{\circ}27' \text{ N}$, $62^{\circ}39' \text{ W}$). 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. The study areas were 4 - 7 km long and had beaches of various sizes. Cavendish Sandspit, Rustico Causeway, and Blooming Point Sandspit included cobble washthroughs and a dynamic dune system, which provided adequate nest habitat. During the breeding season, the nesting areas were closed to human recreational use. Cape Ray Cove in Cheeseman Park ($47^{\circ}37' \text{ N}$, $59^{\circ}16' \text{ W}$) was characterized by an extensive sandy beach about 1.1 km long, in which behaviours of the early arriving birds were observed and noted.

Each area was studied from 06:00 h to 12:00 and for 4 hours before sunset. Each nest was observed behind well-developed dune and noted on locality, sex, nest stage, and general behaviour during one hour. Observations were made to obtain contextual information in which the call was given with $7 \times 35 \text{ mm}$ binoculars and a $20 \times 60 \text{ mm}$ spotting scope. In order to observe detailed responses and calls, a method Simmons (1955) used, which is to lie down or sit down perfectly still more than 15 minutes near a nest, was adopted. The method was more efficient during pairing period, and several

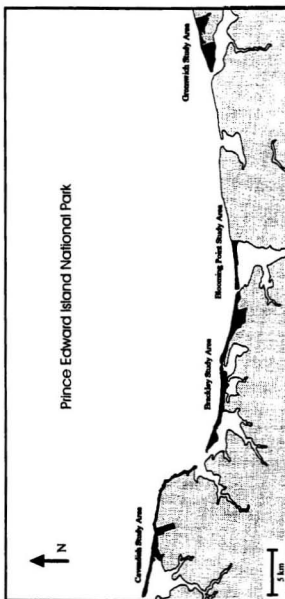


Figure 2.1. Piping Plover study areas (in black) within PEINP

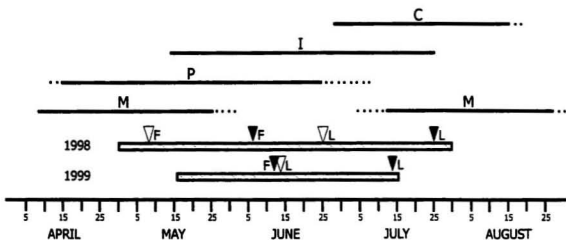


Figure 2.2. Breeding schedule of the Piping Plover at PEINP. C - Parental attendance of chicks; I - incubation; M - migration; P - prenesting. Periods of study in 1998 and 1999 are shown by hatched bars: ∇F - date when first nest was discovered; ∇L - date when last nest was discovered; ▼F - date when first nest hatched; ▼L - date when last nest hatched. (From Thomas et al. 1998, 1999)

pairs kept performing their normal courtship ceremony almost 10 m away from me. At each visit to each site, vocalizations were sampled in several ways. First, all calls uttered by undisturbed birds were noted, and audio recordings were made on an ad hoc basis for one hour. Second, specific call types of target individuals were recorded by waiting until birds were vocally active. Third, after one hour of observation, while walking slowly from the vicinity of one nesting pair to the next pair, vocalizations of encountered birds were recorded. Finally, around the time of hatching, calls of chicks and adults were recorded by placing a dynamic microphone (Turner Co., Cedar Rapids, Iowa, model 2302). The recorder was placed about 100 cm from the nest, and connected to the tape recorder by a long cable. The recorder was hidden by beach debris or a dune. Observation was made simultaneously 10 minutes after the start of the recording to avoid being noticed from high attention of the attending birds. If the birds appeared to be disturbed, recordings and observations were terminated.

The sex of each individual was determined by the length and darkness of forehead and breast plumage, and by bill colour (Haig 1992). Males are darker and have more complete forehead and breast bands, and orange bill than females. In addition, the black tip of the male's bill is less extensive than the female's. The black tip on the female's bill usually occupied 50% or more of the bill's surface area.

Audio recordings were made with a Sony TC-D5PROII tape recorder and a Telinga parabolic microphone. Call analyses were carried out on a personal computer with CSL 4300 and MultiSpeech software (Kay Elemetrics Co., Pine Brook, New Jersey). Calls were digitized at 25 kHz. Each call was measured on temporal (call duration, call

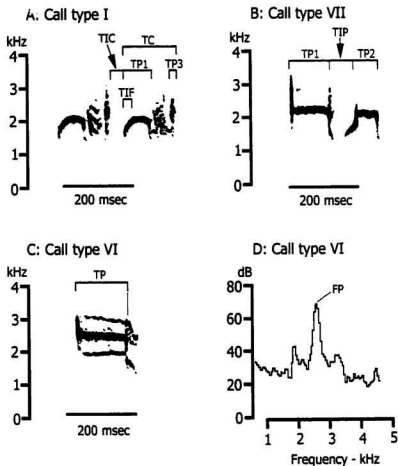


Figure 2.3. Examples of variables used in the study. TC (call duration); TIC (intercall interval); TP (duration of call part); TP1 (duration of first call part); TP2 (duration of second call part); TP3 (duration of third call part); TIP (interval between call parts); TIF (interval from start to peak frequency); FP (dominant frequency of call part). FP of call type VI (D) was shown from the call of sonogram C.

interval, duration of call part, interval between call parts) and frequency variable (dominant frequency; Fig. 2. 3) on spectrograms using a frequency range setting of 600 – 6000 Hz with a wide-band filter of 72 Hz and a Blackman window. The dominant frequency was estimated as the highest average energy within duration on the FFT spectrum.

RESULT

ADULT VOCALIZATIONS

Vocalizations and their probable functions are summarized in Table 2. 1; results of quantitative analyses are presented in Table 2. 2.

Call type I

Call type I was termed "aerial courtship call" by Haig (1992), and has been described variously as "kuk-kuk-kuk" (Pickwell 1925), "bec-bec-bec" (Cairns 1977), or "pipe-pipe-pipe" (Haig 1992). It is a long series of rhythmically repeated calls occurring at an average rate of 4.3 calls per sec; calls averaged 164.5 msec long and intervals between calls averaged 66.5 msec. Each call consisted of three identifiable parts (Fig. 2. 4A): a tonal non-harmonic part; a harmonically rich second part; and a terminal brief broadband part. The first part, initially increased in frequency from about 1.5 kHz to 2.3 kHz in 30 msec, levelled off in frequency, then declined abruptly in frequency; these patterns of frequency change were consistent within individuals but varied among them.

This call usually occurs in advertisement flights (Butterfly Flight) over breeding territories. The calling birds exaggerate their flight figures with slow, deep wingbeats and by rocking the body from side to side. This call often onsets with a series of long, mournful-sounding, call type IV, for 1 - 2 min. During display, call type I is frequently interspersed with call type IV, and less frequently with brief, repeated high- frequency

Table 2.1. Synopsis of adult Piping Plover vocalizations

Call type	Breeding stages	Sexes	Behavioural context	Probable function
I	Pairing, chick care	M	New arrival on prospective territory Intrusion on approach of territory by other breeding plovers Courtship of unmated bird or bird that lost mate	Attracting mate, defending territory, stimulating mating
II	Breeding season	B	Presence of mate Nest exchange Brooding chicks	Stimulating mating Maintaining contact between mates and between parents and chicks
III	Incubation, chick care	B	Approach of ground predator (including human) Brooding chicks Leading chicks to foraging sites	Alerting and distracting intruder Maintaining contact between attending bird and chicks
IV	Breeding season	B	Presence of conspecific birds, predator, or human near nest Inappropriate behaviour of mate or chicks	Alarming Urging to play a relevant role
V	Pairing	B	Presence of mate	Stimulating mating Forming actual nest
VI	Egg-laying, incubation, chick care	B	Approach of ground predator (including human)	Alerting and distracting intruder
VII	Breeding season	B	Presence of ground predator (including human) Flying together during migration Leading chicks to foraging site or finding separated chicks from parents Unmated bird early in breeding season	Distracting intruder Maintaining contact among migrating birds or between parents and chicks Attracting mate (?)
VIII	Pairing, chick care	B	Presence of predator near young Intrusion of conspecific birds into territory	Warn young Alarm
IX	Chick care, post fledging	B	Approach of avian predator or conspecific birds toward young	Alerting and attacking intruder
X	Breeding season	B	Approach of conspecific birds or chick Inappropriate behaviour of mate or chicks	Threatening Urging to play a relevant role

Table 2.2. Quantitative treatment of call types of adult Piping Plovers

Call types and variables (n) ¹⁾	Grand mean \pm SD	Range of individual means	Range of total calls (n) ²⁾
Call type I			
Duration of first call part (9)	93 \pm 14	77 - 116	56 - 136 (382)
Duration of third call part (9)	22 \pm 2	19 - 24	16 - 32 (382)
Interval from start to peak frequency (9)	29 \pm 5	26 - 36	10 - 44 (382)
Call duration (9)	163 \pm 14	144 - 197	103 - 221 (382)
Intercall interval (9)	65 \pm 24	36 - 104	27 - 197 (382)
Dominant frequency of first call part (9)	2155 \pm 124	1927 - 2339	1784 - 2441 (382)
Dominant frequency of third call part (9)	2356 \pm 217	1933 - 2523	1750 - 2912 (382)
Call type II			
Dominant frequency of call (21)	1577 \pm 318	1232 - 2141	875 - 2340 (661)
Duration of call (21)	101 \pm 24	65 - 137	42 - 170 (661)
Call type III			
Dominant frequency of call (11)	1919 \pm 176	1630 - 2171	1531 - 2441 (152)
Duration of call (11)	101 \pm 45	63 - 173	57 - 210 (152)
Call type IV			
Dominant frequency of call (21)	1944 \pm 104	1691 - 2064	1592 - 2138 (248)
Duration of call (18)	776 \pm 162	577 - 1083	100 - 1280 (148)
Call type V			
Dominant frequency of call (2)	2162 \pm 150	2079 - 2211	1683 - 2441 (59)
Duration of call (2)	30 \pm 5	28 - 32	17 - 47 (59)
Interval between calls (2)	124 \pm 25	113 - 143	74 - 199 (52)
Call type VI			
Dominant frequency of call part (51)	2653 \pm 108	2464 - 2893	2340 - 3164 (1426)
Duration of call part (51)	157 \pm 35	97 - 216	72 - 412 (1426)
Call type VII			
Dominant frequency of first call part (42)	2386 \pm 373	1550 - 2743	1144 - 2912 (589)
Duration of first call part (42)	90 \pm 20	65 - 157	39 - 207 (589)
Interval between call parts (42)	70 \pm 28	22 - 114	19 - 228 (589)
Dominant frequency of second call part (42)	2056 \pm 338	1299 - 2419	824 - 2508 (589)
Duration of second call part (42)	91 \pm 51	51 - 241	25 - 331 (589)
Call type VIII			
Dominant frequency of call (36)	2577 \pm 129	2312 - 2868	2003 - 3030 (1376)
Duration of call (36)	65 \pm 10	48 - 83	39 - 108 (1376)
Interval between calls (36)	360 \pm 110	188 - 566	14 - 975 (1273)
Call type IX			
Dominant frequency of call (11)	2204 \pm 185		1851 - 2474 (31)
Duration of call (11)	373 \pm 75		255 - 505 (31)

¹⁾ Sample size in brackets is number of birds.²⁾ Sample size of calls across all individuals.

Frequency variables are in Hz and temporal variable in msec.

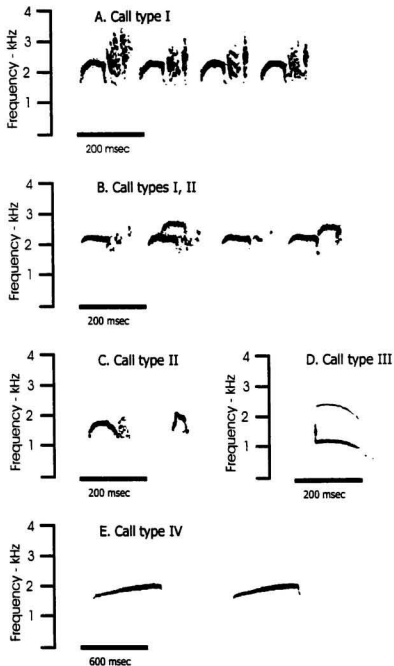


Figure 2.4. Sonograms of Piping Plover vocalizations (part 1/4): (A) - Four calls of a long series from 98-19M on July 10. (B) - Brief, soft calls by female while 99-4M emitted call type I on May 28. (C) - Calls by 98-12F (left) and 98-12M (right) during exchange at the nest on the day of hatching, June 8. (D) - 98-6F's call uttered in distraction display on May 17. (E) - Two calls of a series from 98-12M on May 14.

calls (call type VIII) or rattling calls (call type X). Call type I is often given for several minutes after landing from a display flight.

Aerial displays were performed by newly arrived territorial males engaged in courtship or territorial behaviour, by renesting males, and by males attending chicks. The territorial males showed this display when they were disturbed by other males; e.g. nest-scraping behaviour by an intruder or a nearby aerial display. In particular, renesting males frequently gave this display in response to individuals passing by their territories; males defended their territories until mid July. One male chased other species as well, including Rock Dove (*Columba livia*). Aerial displays lasted several minutes to several hours long with brief resting period on the ground.

In the pre-nesting period, displaying males ended their flights near the females (when present), and began scraping. Aerial displays were often followed by territorial interactions with neighbors, including ground chases, parallel run display, or brief fights, using call types IV and VIII. During a mate's aerial display, the female remained silent nearby or moved to another place within the territory, uttering contact calls (types II or VII; Fig. 2. 4B).

Call type II

Call type II was a brief soft call, used as a contact call between mates and from parent to chicks over short distance (Fig. 2. 4C). It was variable in duration and in patterns of frequency modulation, and differed greatly between both members of a pair.

This call was used by both male and female throughout the breeding season. During

courtship attempts, the calling bird generally emitted slower, lower-frequency continuous calls of “pi-ipe, pi-ipe, pi-ipe’s” (Haig 1992). It often graded into call type I while a tilt display (Cairns 1977; Haig 1992) was performed by the calling male. The female often vocalized in response by intermittently producing this call between the male’s calls and while walking toward the male. The courting male continued to emit the call rhythmically until copulation ended. During incubation and chick care, the pair member arriving to relieve the attending bird gave this call, announcing arrival or departure to the on-duty bird. This call was most frequently uttered during chick care from the onset of hatching for brooding and caring for chicks. Call type VII was often used in the same context.

Call type III

This call was a long call that declined gradually in frequency and typically had a strong second harmonic (Fig. 2. 4D). It was given as a contact call from an attending adult to chicks, and was often mixed with call type VI in distraction displays toward predators (including humans). This call was often the first call part of call type VII in both situations (Fig. 2. 5F). During observations on the broods, it appeared that chicks responded more strongly to this call type than to call type II. For example, one attending bird used this call to lead its chick away, after the chick did not respond to call type II.

Call type IV

This call was described as an alarm call by Haig (1992). It consists of a very soft, long whistle repeated in series, rising gradually in frequency over its length (Fig. 2. 4E). It was given by both sexes from the ground and by the male in aerial display. This call was described as “whooaah whooaah” (Pickwell 1925), “queep-queep-queep” (Cairns 1977) and “woo-up, woo-up” (Haig 1992). Call type X usually preceded this call toward heterospecific and conspecific birds on the ground, while the calling bird kept its body in a horizontal threat posture.

This call is one of the most frequently heard calls during breeding season, and was given in five general contexts: (1) During attempted copulations. One pair member often used this call while approaching the mate. In addition, one female gave this call intermittently without showing any interest in the male's continuous courtship attempts when a Red fox (*Vulpes vulpes*) was nearby. (2) It was elicited by the approach of conspecific birds or predators (including humans) toward the nest. The call was also given upon a bird's hearing call type I or VII near the nest. (3) It was used in hostile encounters on neutral areas, such as small puddles for bathing or feeding. Individuals showed horizontal threat displays (Cairns 1977) to each other while calling. (4) This call was frequently used by the male when he moved between nest-scraping locations. One male gave this call as he returned to his nest for incubation. The male emitted this call followed by a brief call type VIII about 5 m from his nest. (5) It was used when receivers were engaged in biologically inappropriate behaviours. It was observed many times when tending chicks, and four times when chicks were moving instead of crouching

motionless when a predator was nearby. On another occasion, an incubating male flew toward his mate who hesitated during nest-exchange, and showed horizontal threat display with call type IV to his mate.

Call type V

This call was described as nest-scraping call by Haig (1992). It was a series of brief rhythmically repeated calls (Fig. 2. 5A). Haig (1992) described it as being more rapid and of higher frequency than call type I. This call accompanied nest-scraping behaviour during the pre-nesting period. It was given by both members of a pair; call type II was often intermingled. A courting male usually started to scrape first; a female responded with scraping behaviour or by approach. The female's response stimulated the male to move more rapidly from one scrape to another, or to call more intensely in one scrape. The tilt display was performed when the female approached the scrape where the male was.

Call type VI

Call type VI was a brief, loud call (Fig. 2. 5B). The frequency often declined sharply at the end of the call, and harmonics sometimes were evident. It was described as "kee-ah kee-ah" by Pickwell (1925). The call was used by both pair members from egg-laying until fledging period.

This call was directed toward ground predators, including humans, and large birds

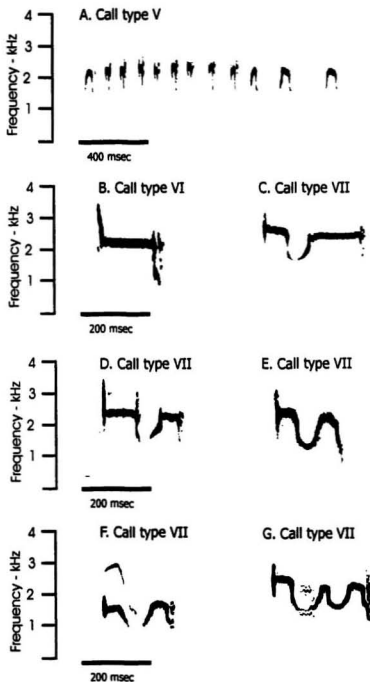


Figure 2.5. Sonograms of Piping Plover vocalizations (part 2/4). (A) - Calls of 98-19M on May 6. (B) - Call of 98-7M on May 20. (C) - Call emitted by unmated male during landing at a probable territory on May 29. (D) - Call of 98-3M during distraction display on May 25. (E), (F), (G) - calls emitted by adult attending chicks on day of hatching (E - 98-19M; F - 98-18F; G - 98-13M).

(e.g. Herring Gulls, *Larus argentatus*, American Crow, *Corvus brachyrhynchos*) feeding near the nest. It occurred during intense distraction displays, such as high-tailed running, crouch-run, and injury-feigning. Use of this call type peaked in the hatching period; aerial calling for distracting potential predators also appeared at this time. High-intensity distraction with use of this call type made the bird conspicuous to predators, and led them away from the nest and chicks. The chicks responded to the call by crouching motionless until the adults gave call types II or VII, or by moving to the opposite direction of the distracting bird.

Call type VI was one of the most frequently recorded call types during the breeding season. Calling birds sometimes also gave call type VII. In one exceptional instance, a male also used call types IV, VII and VIII, and continued in distraction display for 50 m from the nest during egg-laying.

Call type VII

This call consisted of two "parts" which were highly variable in structure according to different contexts and motivational states of the bird (Fig. 2. 5C - G). It was described as "peep-lo" call by Cairns (1997). The call was given in two contexts: (1) During distraction behaviour, the call was often mixed with call type VI. One male in particular used this call for several minutes toward Common Raven (*Corvus corax*) resting near the nest on the day of hatching. (2) It was used as a contact call between mates and from parent to chicks; it was usually given when parents led chicks to the foraging place and when parents searched for separated chicks. During pre-nesting period, paired birds left

the prospective territory soon after one of the pair flew away uttering the call. Finally, the call was also given by pre-migratory individuals in small flocks (sometimes in mixed flocks; e.g. Semipalmated Sandpiper, *Calidris pusilla*). It was frequently observed in birds disturbed from foraging by humans; one or two of the migrating birds took off and started to utter these calls, then other birds followed.

When used with call type II, this call likely functioned to attract females. Once a lone male gave call type VII as it passed over another territory; the resident male uttered call types IV and VIII in response. The lone male continued to utter call type VII when approaching and landing one location and flying to another; after landing, he uttered call types II and VII while walking around. On another occasion, a paired female gave call type VII in response to that of a male flying overhead during the pre-nesting period; the female's mate chased off the lone male.

Call type VIII

Call type VIII consisted of long series of rhythmically repeated, high-frequency brief calls (Fig. 2. 6A). It was performed mainly in two contexts: (1) As a call directed toward conspecific birds, it was recorded most frequently during the pre-nesting period, in particular when birds were in territorial competition. The call was elicited when an individual or group of shorebirds, including Piping Plovers, was foraging near the territory. The responding bird (usually the male) flew toward the other birds with this call. After landing, the bird kept calling with erect postures and head-bobbing, often followed by parallel run display. In addition, it continued to chase the intruders with

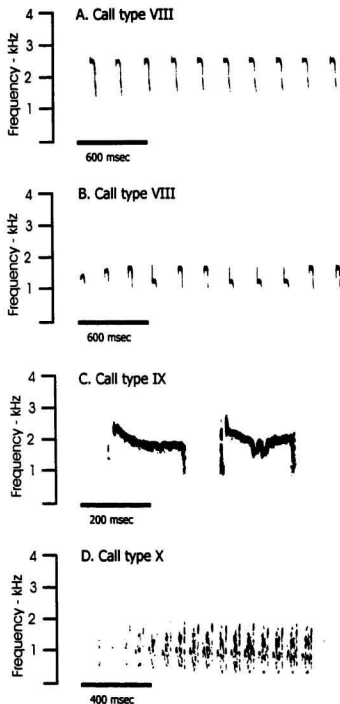


Figure 2.6. Sonagrams of Piping Plover vocalizations (part 3/4). (A) - Calls of a series from 98-22F on June 22. (B) - Calls of a series from 98-12M on May 14. (C) - Calls of 98-15M on a day of hatching. (D) - 98-5M emitted calls with horizontal threat posture toward his mate on a day of hatching.

horizontal threat charges on the ground with call types IV and X. Ground chasing often merged into aerial chasing. Such calling behaviour was also observed in newly arrived adults, for example, four individuals (probably two pairs) in prospective nesting areas. The pairs repeatedly performed behaviour like that described above over a period of several hours, and which included brief fights. (2) As a warning call to chicks, the call was used by both members of a pair frequently during the period of chick care. Some sequences exhibited sub-sequences of high- and low-frequency calls (Fig. 2. 6B). Birds emitted this call type when they saw potential predators approaching on the ground near the chicks (including humans and Common Raven); calling continued until the predators left. Chicks responded to this call by crouching motionless or moving with "stop-and-run" motion from feeding to hiding places. The calling bird directed the call to the chicks, and at the same time made itself visually conspicuous to the predators while calling. The duration of calling differed between the two contexts: the calls emitted with relation to latter context were relatively longer.

Call type IX

This call was a high-frequency whistle with a sharp onset and offset, and variable patterns of frequency modulation (Fig. 2. 6C). It was given by both sexes that had chicks when aerial predators were passing by or appeared suddenly near the chicks. In particular, when the pairs were extremely sensitive and aggressive toward other species on hatching day, the calls were given more frequently. The calling bird often flew toward and chased low passing avian intruders including Common Raven, Herring Gull

and Common tern (*Sterna hirundo*). During aerial chasing this call type sometimes resembled call type VII or brief call type VI.

Call type X

This call consisted of rhythmically repeated brief broadband calls (Fig. 2. 6D), often followed by call type IV. Cairns (1977) described it as a series of low, rattling “bec-bec-bec” calls. This call was given by both males and females throughout the breeding season. The calling bird maintained a horizontal threat posture, with slightly raised wings and puffed feathers, to the target bird in aggressive contexts. The call was directed toward invading shorebirds of similar size, and sometimes toward the mate or chicks when they showed biologically inappropriate behaviour (see call type IV).

CHICK VOCALIZATIONS

Call type I, II

Three different call types of Piping Plover chicks were identified; two (call types I, II) were produced within one day of hatching (Fig. 2. 7). Call type I was an extended long whistle with gently rising frequency near its termination; such a frequency pattern makes localizability difficult (Marler 1955). The call varied in frequency and duration (Table 2. 3). It was recorded when the chicks wandered near the attending adult on the

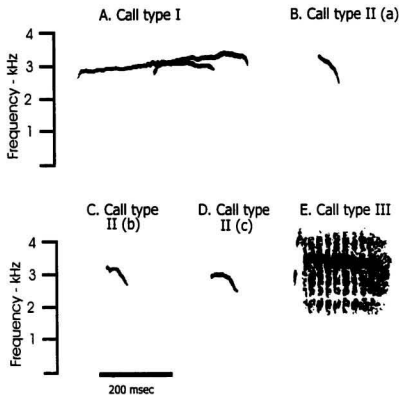


Figure 2.7. Sonograms of Piping Plover vocalizations of chicks (part 4/4). Call type I and call type II (a), (b) were emitted during hatching day, (c) at 25 days after hatching, and call type III during in hands. The sonogram of call type I shows two calls given simultaneously by two chicks.

Table 2.3. Quantitative treatment of call types of chick Piping Plovers¹⁾

Call types and variables	Grand mean \pm SD	Range of total calls (n) ²⁾
Call type I		
Dominant frequency of call	3067 \pm 236	2643 - 3535 (23)
Duration of call	361 \pm 120	86 - 489 (23)
Call type II		
Dominant frequency of call	3121 \pm 222	2390 - 3484 (53)
Duration of call	79 \pm 21	39 - 147 (53)
Call type III		
Dominant frequency of call (3) ³⁾	3662 \pm 226	3198 - 3939 (23)
Duration of call (3)	261 \pm 55	135 - 327 (23)

¹⁾ Samples of call type I, II were collected in five nests. Frequency variables are in Hz and temporal variables in msec.

²⁾ Number of calls.

³⁾ Number of chicks.

day of hatching; subsequently it was not possible to record chicks or to approach them closely enough to detect this soft call type. Call type II was a brief call of decreasing frequency, heard most frequently throughout the period of chick care. Chicks gave this call while wandering around the nesting or feeding area; presumably it functioned to maintain contact with the parents. Call type II (c) in Fig. 2.7 was given by a chick seeking its parent after being alone in the foraging area sometime. This call type showed a slight change in form from an early age when it usually declined in frequency from the onset. The two call types were given when chicks were in undisturbed situations, especially as a chick wandered away from its parent. The chick and its parent often counter-called, with adults giving call type II, III, or VI.

Call type III

This call consisted of a series of rapid high-frequency trills of broadband pulses (Fig. 2. 7E). Features make a call easily located. The call type was given when a chick was held in the hand for banding. On being caught, the parent stayed near and usually uttered call type VII. In addition, one parent flew to pursue the Common Raven, which preyed on the chicks, for a while with uttering call type VII.

DISCUSSION

Repertoire size

The vocal repertoire of adult Piping Plovers includes at least 10 distinct call types during the breeding season. The size of the vocal repertoire in this species was similar to that of other *Charadrius* species, which have eight to 12 call types or groups (Table 2. 4). Compared with other non-passerine families, the Piping Plover is intermediate (with other shorebirds) between petrels and highly social species such as Red Junglefowl and passerines.

There is always difficulty in counting types of vocal signals due to variable graded vocalizations. For instance, Ficken et al. (1978) identified 11 vocalizations in the Black-capped Chickadee, but admitted that slightly different information might be transmitted by variants within one highly variable category (Chick-a dee calls). In addition, vocalizations of Killdeer, which consisted of highly graded signals, were divided into 12 call categories composed of 19 note types, but only one distinct type was found (Bursian 1971). Green (1975) and Maier (1982) analyzed these graded sounds by considering behavioural patterns of the sender and the principal circumstances in which the sounds were used, as well as the responses of the receivers; they thus went beyond acoustic properties to contextual and functional considerations in arriving at the classifications. Riska (1986), in his study of Brown Noddy vocalizations, identified nine

Table 2.4. Comparison of the number of vocal signals in adults of selected species of birds

Family and Species	No. of vocal signals	Reference
Alcidae		
Ancient Murrelet (<i>Synthliboramphus antiquus</i>)	9	Jones et al. 1989
Pigeon Guillemot (<i>Cephus columba</i>)	9	Nelson 1985
Hydrobatidae		
Leach's Storm-Petrel (<i>Oceanodroma leucorhoa</i>)	3	Taoka et al. 1988
Wilson's Storm-Petrel (<i>Oceanites oceanicus</i>)	4	Bretagnolle 1989
Scolopacidae		
Green and Solitary Sandpipers (<i>Tringa ochropus</i> and <i>T. solitarius</i>)	7	Oring 1968 ¹
Willet (<i>Catoptrophorus semipalmatus</i>)	10	Sordahl 1979
Long-billed Curlew (<i>Numenius americanus</i>)	8	Forsythe 1970
Little Curlew (<i>Numenius minutus</i>)	7	Vepintsev and Zablotskaya 1982
Whimbrel (<i>Numenius phaeopus</i>)	10	Skeel 1978
Charadriidae		
Kentish Plover (<i>Charadrius alexandrinus</i>)	9	Cramp et al. 1983, Krey 1991
Double-banded Plover (<i>Charadrius bicinctus</i>)	6	Phillips 1980 ²
Little Ringed Plover (<i>Charadrius dubius</i>)	10	Cramp et al. 1983
Ringed Plover (<i>Charadrius hiaticula</i>)	9	Cramp et al. 1983
Piping Plover (<i>Charadrius melodus</i>)	10	This study
Lesser Sand Plover (<i>Charadrius mongolus</i>)	8	Gebauer and Nadler 1992
Mountain Plover (<i>Charadrius montanus</i>)	10	Graul 1974
Killdeer (<i>Charadrius vociferus</i>)	12	Bursian 1971
Wilson's Plover (<i>Charadrius wilsonia</i>)	8	Bergstrom 1988a
Jacaniidae		
Northern Jacana (<i>Jacana spinosa</i>)	6	Jenni et al. 1975
Sterninae		
Brown Noddy (<i>Anous stolidus</i>)	9	Riska 1986
Recurvirostridae		
Avocet (<i>Recurvirostra avosetta</i>)	10	Adret 1982
Phasianidae		
Scaled Quail (<i>Callipepla squamata</i>)	11	Anderson 1978
Red Junglefowl (<i>Gallus gallus</i>)	19	Collias 1987
Corvidae		
Azure Jay (<i>Cyanocorax caeruleus</i>)	14	Anjos and Viellard 1993
Common Raven (<i>Corvus corax</i>)	18	Conner 1985
Australian Raven (<i>Corvus coronoides</i>)	18	Rowley 1973
Titmice		
Boreal Chickadee (<i>Parus hudsonicus</i>)	18	McLaren 1976
Black-capped Chickadee (<i>Parus atricapillus</i>)	11	Ficken et al. 1978
Great Tit (<i>Parus major</i>)	40	Gompertz 1961
Pipridae		
Long-tailed Manakin (<i>Chiroxiphia linearis</i>)	13	Trainer and McDonald 1993

¹ Oring (1968) divided them into two song types and five calls in both species.

² Phillips (1980) classified vocalizations of this species into six types, but his research concentrated on agonistic and sexual behaviour.

temporally different calls consisting of high graded vocalizations. These calls showed significant differences in measured call features on sonograph and in their contexts in which the call was given. Collias (1989) recognized about 24 different calls in Red Junglefowl by seeking common elements in various situations in which the signals were given. Analyses of graded vocal signals of birds and primates therefore emphasize the multiplicity of approaches that can be used to detail a species' repertoire. This needs to be borne in mind when comparing studies.

Nevertheless, approximate repertoire size and organization reflect similarity of vocal functions under similar ecological pressures, like open habitats. Firstly, alarm calls may constitute the main functional categories of vocalizations of open-country species because of vulnerability to predators, and the visual ability to detect predators. Klump and Shalter (1984) defined the general term "alarm calls" as including four categories with possibly different functions: (1) mobbing calls, (2) alarm calls (warning calls and pursuit-inhibition or pursuit-invitation calls), (3) distress call or defense calls, and (4) distraction calls. According to this categorization, five (call type IV, VI, VIII, IX, and X) out of 10 call types of Piping Plovers could be considered as alarm calls. Call types IV and X are likely classified as defense calls, call type VI as a distraction call, call types IV and VIII as warning calls, and call type IX as a pursuit-inhibition call. Because of the possibility to have more than one function, call type IV and VIII can be classified in two categories. Similarly, seven of 10 call types in Mountain Plover

(*Charadrius montanus*; Graul 1974), four of eight in Wilson's Plover (*C. wilsonia*; Bergstrom 1988a), and four of nine in Ringed Plover (*C. hiaticula*; Cramp et al. 1983) fit the category of alarm calls. The distraction call is seemingly a universal call of *Charadrius* plovers. Alarm call is also a major category of many scolopacid vocalizations; five or six of eight adult call types in the Long-billed Curlew (Forsythe 1970), four of eight in Little Curlew (Veprintsev and Zablotskaya 1982), and at least five of 10 in Whimbrel (Skeel 1978).

Vocalizations of Piping Plover were often presented and simply mixed with other call types in single behavioural context. For instance, territorial males frequently gave call types IV and IX to conspecific birds on the ground, and call types I and IV, I and VII, I and IX in the air. However, each of the two call types was also uttered separately in similar circumstances. The use of mixed call types may depend on ambivalence of the motivational state of caller (i.e. the possible function of the aerial courtship calls). Alternatively, two call types could perform different functions. For instance, the approach of a predator to chicks released call type VIII followed by call type VI, with call type VIII directed to chicks and call type VI to the predator.

Collias (1960) showed that physical attributes of mate-attraction and parental contact calls are similar. Vocalizations of Piping Plover show similar trends. Call type II was used as a contact call between mates, between parent and chicks, and also used during copulation attempts. When being used by courting male, the call often graded into call type I.

Adaptation of vocal signals to open habitats

The vocal repertoire of *Charadrius* species studied to date mainly comprises discrete sounds except for that of Killdeer. Some kinds of vocalizations may be valuable in studies of adaptation or phylogeny. Structure and usage of vocalizations of *Charadrius* species were compared based on similarity of sonagrams and written descriptions (Table 2. 5).

Table 2. 5 shows that *Charadrius* species have broadly similar calls with similar functions (Collias 1960). For example, the call used as a contact call between mates or parents and chicks consists of one part with inverted V, U or M shape, or often has two parts. One-part contact calls also occur in Green and Solitary Sandpipers (Oring 1968), and are similar to the 'parental rallying call' and the 'chuckle' call of Avocet (Adret 1982), and the 'food call' of the Red Junglefowl (Collias 1989). In Whimbrel, the 'adult-to-chick contact call' is a low frequency gurgling trill. A similar call has been reported in Mountain Chickadee, in which Category I including single, arch-shaped elements was classified as close-range, contact calls (*Parus gambeli*; Gaddis 1985). In addition, the 'broken Dee' call and 'begging Dee' call of the Black-capped Chickadee (Ficken et al. 1978) are structurally similar. Two-part calls functioning as contact calls are structurally similar to the 'chekar' call of the Scaled Quail (Anderson 1978) and the 'attraction calls' of a hen to chicks of the Red Junglefowl (Collias 1989). Even if it is whistle shaped notes, the 'curluoo' call of Long-billed Curlew (Forsythe 1970), the 'kyah-

Table 2.5. Comparison of structure and function of vocalizations in adults of *Charadrius* species ¹⁾

	<i>alexandrinus</i>	<i>bicinctus</i>	<i>dubius</i>	<i>hiaticula</i>	<i>Melodus</i>	<i>mongolus</i>	<i>montanus</i>	<i>wilsonia</i>
A. 1 – note call								
1) Inverted V, U or M shape	Contact ¹	Moderate / low states of excitement; brooding; contact	Intermediate form from general contact and alarm to assembly call		Contact; mating (Call type II, III)	Flight call left due to disturbance	Brooding	Nest relief
2) unmodulated shape of high frequency	Distracting ²				Distracting predator (VI)	Distracting	Injury-feigning display	Broken wing display
of low frequency (below 2 kHz)		Courtship display					Courtship display	Courtship display
3) Increasing or decreasing frequency	Alarm-threat or excitement	Advertising ³	Alarm-threat; general contact; alarming or warning ⁵	General contact & alarming; alarm-threat	Urgent alarming; general alarming (IV, IX)	Excitement by human disturbance; lure	Anxiety movement; aggressive encounters	Alarming
B. 2 – note call	Parent-young contact		Contact call		Contact; leading chicks (VII)	Contact; flight call left due to disturbance ⁷		
C. Chattering call								
1) With similar interval		Butterfly flight ⁴	Demonstrating & distraction behaviour by adults with young		Ground-predator alarming; warning to intruder (VIII)	Distracting	Aerial chasing; moving toward intruder	
2) With repeated brief note group	Alarming		Scraping-call		Nest-scraping (V)	Excitement by human disturbance	Moving toward intruder	
D. Trill call *	Threat		Hostility-cry	Threat	Threatening (X)	Territorial call		Ground & aerial chasing
E. Note complex call	Display-song in flight; threat	Threatening or attacking males	Flight-song ⁶	Song; threat	Advertising (I)			

¹⁾ *Charadrius alexandrinus* (Cramp et al. 1983; Krey 1991), *bicinctus* (Phillips 1980), *dubius* (Cramp et al. 1983), *hiaticula* (Cramp et al. 1983), *mongolus* (Gebauer and Nadler 1992), *montanus* (Graul 1974), and *wilsonia* (Bergstrom 1988a).

* Trill call clearly distinguished from chattering call by note features: the calls consist of brief clicks and note form is not clear like call type X of Piping Plover.

¹ The call was described as monosyllabic version of parent-young contact call- "purrr" without a sonagram (Walters 1957).

² The call shows intense buzzing calls with harmonics.

³ Phillips (1980) interpreted "Tic Whee-o-whit (WOW)" as advertising call, which was frequently used to passing *bicinctus* by unmated males early in the nesting cycle.

⁴ Phillips (1980) noted that Butterfly Flight display of this species differs from that of *vociferus*, *dubius* and *hiaticula*.

⁵ In case of intense alarm-threat call, the call is shorter in duration and shows asymmetrically inverted v-shapes.

⁶ Although other types can be uttered with song or advertising call, main call was adopted.

⁷ The first note is relatively brief, and almost merges with the second note.

⁸ This call was expressed as "mooing call" during the Scrape-ceremony, and described in *wilsonia* without a sonagram (Bergstrom 1988).

yah' call of Willet (Sordahl 1979), and the 'faint Fee-bees' of Black-capped Chickadee (Ficken et al. 1978) have comparable function.

Gently rising or decreasing frequency occurred in calls used in various behavioural contexts and may serve more than one function. One possible function is to threaten or alert predators or conspecifics. Calls similar to the call type IV of the Piping Plover are the 'wee-wee call' of the Mountain Plover (Graul 1974), 'weep-weep', 'queep', or 'tjooeep' calls of Ringed Plover (Cramp et al. 1983), 'Tweet' call of Wilson Plover (Bergstrom 1988a), 'hooet' call of Kentish Plover (Cramp et al. 1983), and 'w(-)eer' or 'tee(-)u' calls of Little Ringed Plover (Cramp et al. 1983). Similar calls are the 'alarm-flee' of Green and Solitary Sandpipers (Oring 1968) and 'tsing' call of Scaled Quail (Anderson 1978). These calls were similar in being long calls of slowly ascending or descending high frequency, which gives low localizability (Marler 1955). Similar calls appear in chick vocalizations (Table 2. 3). Another function in Piping Plover is to signal to the mate or chicks to engage in relevant behaviours. Interestingly, there is a report that the Little Ringed Plover gave the call on approach of its partner in the early days of pairing (Cramp et al. 1983). Furthermore, this call is frequently given during chick care, in particular during the exchange of parental duties. Such a contextual behaviour has been also reported in the 'Tweet' call of Wilson's Plover (Bergstrom 1988b).

In birds and mammals, alarm calls to terrestrial predators have been characterized as locatable 'chats', 'chatters', and to aerial predators as non-locatable 'whistles' (Gyger et al. 1986; Owings and Virginia 1978). This generalization applies to alarm calls of Piping Plover: Call type VIII for terrestrial predators, and call type IX for aerial predators. A calling bird giving call type IX should be more easily located than call type IV because the former was loud and had greater bandwidth due to frequency modulation (Simmons 1973). Thus, the call can attract a predator's attention to the emitter, and startle the predator and increase its reaction time (Humphries and Driver 1967), or signal to the predator that it has been detected. The cock of Red Junglefowl similarly utters a loud 'scream', which is a mixed call with low- and high-frequency components (Collias 1987). In Avocet, the 'alarm whistle' call is used in the same situation. Birds giving chattering calls are easily located because of the repeated brief calls (Marler and Hamilton 1967). Furthermore, the causes eliciting these two different call types have been widely discussed with relation to predator types and response urgency (Macedonia and Evans 1993; Blumstein and Armitage 1997). Observations of the behaviour of the Piping Plover suggest that it use different types of calls based on response urgency rather than on predator type. For example, a parent uttered chattering calls on seeing the Raven feeding at a great distance, but emitted 'whistle' calls to Ravens or other potential predators flying over their chicks. The response of Red Junglefowl to a hawk is similar (Collias 1987). Calls equivalent to Piping Plover call type VIII in the Green and Solitary

Sandpipers is the 'alarm-attack' call. In other scolopacids, the 'Kleep' call of Willet (Sordahl 1979), 'ki-keck' call of Long-billed Curlew (Forsythe 1970), and 'scolding trill calls' of Whimbrel (Skeel 1978) are similarly used in mobbing.

Calls used in distraction displays are similar in different *Charadrius* species. The 'squeal' call of Mountain Plover (Graul 1974), 'distraction' call of Wilson's Plover (Bergstrom 1988a), Lesser Sand Plover (Gebauer and Nadler 1992), and Kentish Plover (Cramp et al. 1983) show close similarity with Piping Plover call type VI. It is described as a harsh, croaking 'rarr rarr' in Little Ringed Plover (Dathe 1953) and as a resonant, grating croaking call 'kewrr-kewrr-kewrr' in Ringed Plover (Witherby 1940). It is a very loud, relatively high-frequency call with harmonics over a broad frequency range, so is easily located (Marler 1955).

Call type I used in advertisement flight or Butterfly Flight was composed of two or three different kinds of notes produced as a loud, rhythmically repeated call. It has been suggested that nuptial vocalizations are innate and stereotyped vocal signals adapted for long-distance transmission in open, windy environments (Wiley and Richards 1982; Miller et al. 1984; Miller 1996a). The structure and function of shorebird vocalizations also have potential for clarifying evolutionary relationships, because of their similarity across species (Ferdinand 1966; Dabelsteen 1978; Miller 1983, 1996b). For example, Butterfly Flight calls of Ringed and Semipalmated Plovers (*Charadrius semipalmatus*) are similar in having tripartite structures and the same sequence (Miller 1996a). Such similarities appear in call type I of Piping Plover, and the comparable calls of

Little Ringed Plover; Killdeer calls show some similarities. However, there were differences in fine features of the calls. The rest of the tonal and non-harmonic part showed different features according to the species: In Piping Plover, it is a brief broadband element, in Ringed and Semipalmated Plovers it is longer and harmonically rich, in Little Ringed Plover it is trill-like, and in Killdeer it is a briefly inverted-v-shape call.

Vocalizations and pair formation

The function of advertisement flight is mate attraction or territorial defense (Armstrong 1963). Cairns (1977) suggested that the Butterfly Display of Piping Plover plays a greater role in courtship than in territorial aggression, but Simmons (1953) regarded it to have an aggressive function in Ringed and Little Ringed Plovers. The fact that unmated males or males that lost their mate gave call type I in Butterfly Flight or directed toward other conspecific females shows that it functions in mate-attraction or courtship. However, males also used the call with Butterfly Display after the chicks hatched, and paired males with their mates gave it either when chasing conspecific birds or heterospecific birds. In addition, it was often given with high intensity between nest-scraping calls on the ground. I conclude that it has broad sexual and aggressive-territorial functions.

Unmated males or males after losing the mate displayed in two ways. One was to remain on site and wait for passing females. Such males frequently used call type I interspersing call types IV and VIII for advertisement display to any

passing conspecific birds. The other strategy was to visit other possible territories uttering call type VII. Such wandering males were observed more frequently in 1999 than 1998. In 1999, more pairs lost eggs and nests because of severe environmental conditions (storms; strong wind) and through predation (Thomas et al. 1998, 1999).

CHAPTER 3. INDIVIDUAL AND SEXUAL DIFFERENCES IN VOCALIZATIONS OF PIPING PLOVERS

INTRODUCTION

Vocal individuality is a prerequisite for individual recognition and can be a valuable management tool, especially for rare or uncommon species. Individual recognition between pair members, relatives, or neighbors is important in many social circumstances (Wanker et al. 1998; Wiley and Wiley 1977; Colgan 1983; Beecher 1988, 1989; Ydenberg et al. 1988; Studholme 1994). Individualistic features of vocalizations have also been used effectively as a census tool for diverse species: American Woodcock (*Philohela minor*; Beightol and Samuel 1973), Bald Eagle (*Haliaeetus leucocephalus*; Eakle and Mannan 1989), Eurasian Pygmy Owl (*Glaucidium passerinum*; Galeotti et al. 1993), Arctic Loon (*Gavia arctica*) and Great Bittern (*Botaurus stellaris*; Gilbert et al. 1994), Northern Saw-whet Owl (*Aegolius acadicus*; Otter 1995), Marbled Frogmouth (*Podargus ocellatus*; Jones and Smith 1997), and Corn Crane (*Crex crex*; Peake et al. 1998).

The Piping Plover (*Charadrius melodus*) was listed as an endangered species in Canada in 1985 and as a threatened and endangered species in USA since 1986 (Haig 1992). It has a broad but highly disjunct breeding range: The species nests over a large area in the Great Plains, and also on beaches of Atlantic provinces and states (American Ornithologists' Union 1998; Haig 1992). Within these two large areas, nesting distributions are fragmented and local populations are often small. As one technique for management and conservation, vocalizations may be used to monitor

population trends and size if vocalizations satisfy two criteria: high variation among and little variation within individuals (and sexes); and vocal constancy within and across years (Falls 1982; McGregor and Byle 1992).

The species has several characteristics that make it a good subject for such an application. As the species is socially monogamous and both members of a pair defend the territory, it is easy to distinguish males from females based on their plumage and bill colour, and to distinguish intruding males based on agonistic behaviour. Furthermore, Piping Plovers show fairly high fidelity to nesting sites in successive years, and have several distinctive call types that can be readily recorded and identified. Shorebirds probably do not learn their vocalizations so vocal characteristics are expected to be consistent over years (Miller 1984, 1992). Finally, the fragmented breeding distribution and locally small nesting populations make enumeration and vocal identification a relatively easy task.

The main goals of this study were to describe individual and sexual variations in selected vocalizations, and evaluate the potential for vocal individuality as a management tool (e.g. for monitoring long-term changes in populations).

METHODS

Study area and recordings

Research was conducted in and near Prince Edward Island National Park (PEINP; 46°25' N, 63°13' W) from 1 May to 30 July 1998 and 17 May to 15 July 1999. Ten classes of vocalizations have been recognized (see first chapter). Call types I, VI, VII, and VIII were selected for this study because they were easily recorded and formed fairly discrete classes. Call type I is a long series of rhythmically repeated calls, and consists of three identifiable parts: a tonal and non-harmonic part, a harmonically rich second part, and a terminal brief broadband part. Most calls are accompanied by advertisement flights over breeding territories. Call types VI and VIII consist of monosyllabic calls, which are directed toward ground predators, including humans, and large birds (e.g. gulls or crows). Call type VII consists of two call parts, which are mainly used as a contact calls between mates and from parent to chicks.

Recordings were made from 06:00 h to 12:00 and for 4 hours before sunset. Each nest was observed, and notes on location, sex of individuals, nest stage, and general behaviour made for one hour. Observations were made with 7 × 35 mm binoculars and a 20 × 60 mm spotting scope. At each visit to each site, vocalizations were sampled in several ways. First, all calls uttered by undisturbed birds were noted, and audio recordings were made on an ad hoc basis for about one hour. Second, specific call types of target individuals were recorded by waiting until birds were vocally active. Third, after one hour of observation, while walking slowly from the vicinity of one nesting pair to the next pair, vocalizations of disturbed birds were

recorded. Efforts were made to record vocalizations at different stages of breeding, the days before and after hatching, and on the day of hatching. The individuals on the same territories within breeding seasons were recognized by behavioural idiosyncrasies and strong territorial behaviours; four PEINP staff checked territories daily and confirmed their continued occupancy. Three females and two males were captured and banded in 1998 by the Canadian Wildlife Service (CWS). Extensive recordings of these individuals were made in 1998. One male returned, and calls of types VI and VIII were recorded in 1999.

The sex of each individual was determined by the length and darkness of forehead and breast plumage, and by bill colour (Haig 1992). Males are darker and have more complete forehead and breast bands, and oranger bill than females. In addition, the black tip of the male's bill is less extensive than the female's. The black tip on the female's bill usually occupied 50% or more of the bill's surface area.

Audio recordings were made with a Sony TC-D5PROII tape recorder and a Telinga parabolic microphone. Call analyses were carried out on a personal computer with CSL 4300 and MultiSpeech software (Kay Elemetrics Co., Pine Brook, New Jersey). Calls were digitized at 25 kHz. Each call was measured on temporal (call duration, intercall duration, duration of note part of the call) and frequency (dominant frequency) variables. The measurements were made on spectrograms using a frequency range setting of 600 – 6000 Hz with a wide-band filter of 72 Hz and Blackman window.

Data analysis

Temporal measurements were made to the nearest 1.68 msec from spectrograms and dominant frequency was estimated as shown in Fig. 3. 1D, using a power spectrum displayed in bar mode; frequency was measured to 16 Hz. Variables were:

Call type I. Temporal (T-) variables (Fig. 3. 1A): Total duration across three call parts (TC/I); durations of first (TP1/I) and third (TP3/I); interval between successive calls (TIC/I). Frequency (F-) variables: Dominant frequency of first (FP1/I) and third (FP3/I) call parts.

Call type VI. T- variables (Fig. 3. 1C): Duration of call part (TP/VI); total duration and duration of terminal part were not measured because the part was often faint. F- variables (Fig. 3. 1D): Dominant frequency of call part (FP/VI).

Call type VII. T- variables (Fig. 3. 1B): Durations of first (TP1/VII) and second (TP2/VII) call parts; interval between call parts (TIP/VII). F- variables: Dominant frequency of first (FP1/VII) and second (FP2/VII) call parts.

Call type VIII. T- variables: Total duration (TC/VIII); interval between successive calls (TIC/VIII). F- variables: Dominant frequency of call (FC/VIII).

Means and coefficient of variation (CV) were calculated for each variable within individuals, and an average within-individual coefficient of variation (CV_w) was computed. An among-individual coefficient of variation (CV_a) was calculated from those means. The ratio $CV_a / \text{mean } CV_w$ provides a measure of individuality (Jouventin 1982; Bretagnolle 1989). Vocal differences among males for call type I were estimated using one-way ANOVA. Differences among individuals within and between sexes for call types VI, VII, and VIII were tested using nested GLMs. The

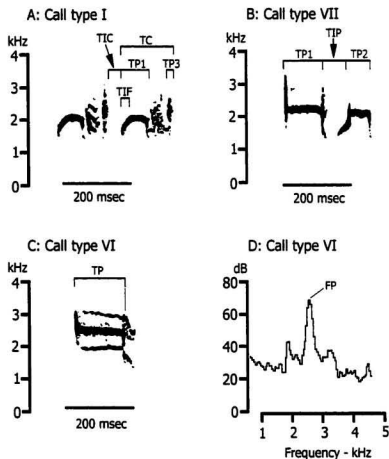


Figure 3.1. Examples of variables used in the study. TC (call duration); TIC (intercall interval); TP (duration of call part); TP1 (duration of first call part); TP2 (duration of second call part); TP3 (duration of third call part); TIP (interval between call parts); TIF (interval from start to peak frequency); FP (dominant frequency of call part). FP of call type VI (D) was shown from the call of sonagram C.

variance components were used to estimate the percentage of the variation at each level in the analysis. Autocorrelation tests were performed to examine sequential effects in call types I and VIII. The calls were randomly sampled from bouts for each individual, and the correlation of a series of calls for each frequency and temporal variable was calculated; a t-statistic was used to test whether or not a lag equaled zero; a default number was selected by the program with $n/4$, where n is the number of calls in the series.

To investigate seasonal variation within individuals, call types VI and VII were compared across three stages of nesting: pre-hatching; day of hatching or hatching period; and post-hatching. For call type VII, hatching period was considered to be a 7-day period beginning on the day of hatching, seemed highly excitable and responsive to human intrusion for about that long. Both adults usually tend the brood during the first week after hatching; after that one adult tends while the other bird feeds or rests (Cairns 1977). Whyte (1985) argued that the first week might be the most critical period for chick survival. Therefore, it is expected that the adults will be more dependent on closer communication with chicks during the first week.

StatView V. 5.0 (SAS Institute) was used for descriptive statistics and one-way ANOVAs, Minitab V. 10.2 for autocorrelation, SAS V. 6.12 for nested GLMs and variance component, and S-plus V. 4.5 for multiple comparisons and classification trees. For small sample sizes, if the residuals were not normal, data transformation or nonparametric methods were used. Furthermore, a sequential Bonferroni correction was performed to lower the type I error for each comparison (Sokal & Rohlf 1995).

Classification tree analysis was used to re-identify calls of one male plover that was banded on its nest in 1998 and returned to breed in 1999. This analysis has been

suggested to be a useful tool for devising decision rules to classify subjects into relatively homogeneous groups (Clark and Pregibon 1992; Iverson et al. 1997; Smith et al. 1997). The best variable is selected as a decision rule for splitting the data into two groups at each node based on the deviance, a measure of node heterogeneity. Data splitting continues recursively until either the minimal node size is < 10 or the minimal node deviance is < 0.01 . After a tree is created, the misclassification error rate is calculated by the improperly assigned numbers divided by the total number of observations. Reducing the terminal nodes results in increasing the misclassification rate. To predict adequate tree size, a cross-validation method was used.

RESULTS

INDIVIDUALITY IN CALL TYPE I

Vocal differences among males

Call type I was recorded from 13 males. Sonagrams could be readily assigned to these individuals based on general appearance (Figs. 3. 2, 3. 3). Individualistic features are apparent in the frequency pattern of the first call part and duration plus spectral features of the second and third parts. For instance, male 99-5M (Fig. 3. 2H) showed a gradual then sudden decline in frequency after peak frequency was reached in the first call part; this frequency pattern was unique among the 13 males. Sonagrams of male 98-30M (Fig. 3. 2G), 98-17M (Fig. 3. 2E), and 98-19M_July 10 (Fig. 3. 3F) were equally distinctive in general features of the second and third call parts.

Means and CVs are summarized in Table 3. 1. TIC varied most within individuals (CV range, 8 - 29 %) and FP1 varied least (CV range 1 - 4 %). The CV - ratios revealed high call individuality for each variable except TP3 (Table 3. 2).

Vocal differences of call type I between the two periods

Calls of 98-16M and 99-1M were recorded on different dates in 1998 and 1999. The sonagrams are similar between periods for each male (Fig. 3. 3). Calls of 98-16M kept a smoothly changing frequency pattern at the anterior of the first call part, and showed an inverted v-shape note in under portion between second and third call part. Vocalizations from different periods are compared in Table 3. 3. One-way ANOVAs revealed some statistically significant differences between periods.

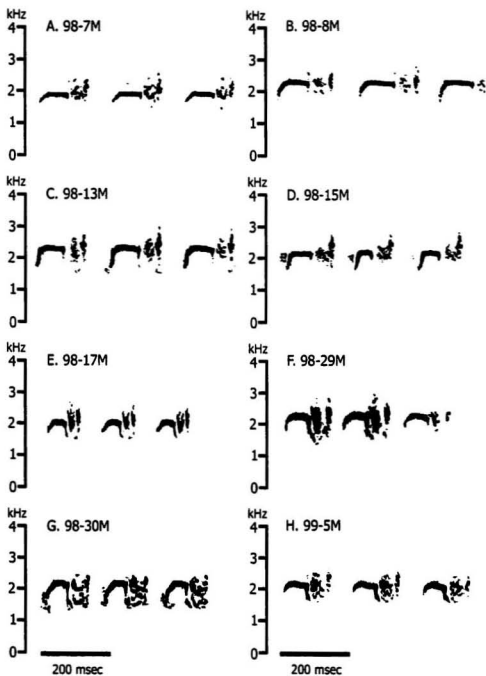


Figure 3.2. Sonograms of call type I showing differences among individuals.

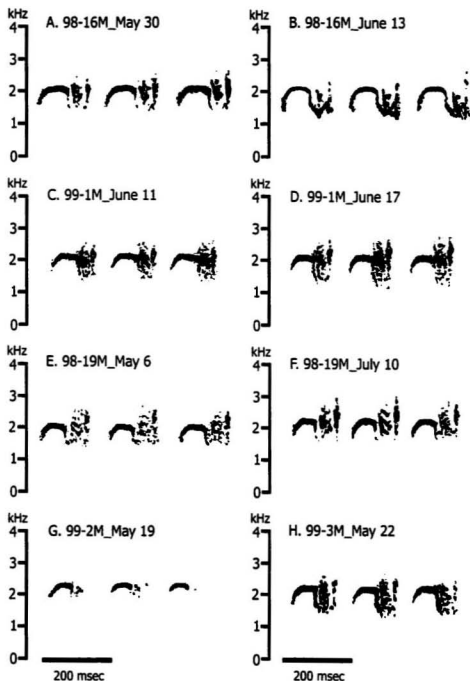


Figure 3.3. Sonograms of call type I recorded within the same territory of different periods: (A) and (B), (C) and (D), (E) and (F) show similarities between two periods of 1998, despite the fact that (E) were given on the ground, and (F) were aerial. (G) and (H) were present on the same nesting area of 98-19M in 1999: 99-2M disappeared after losing his mate, and 99-3M occupied the same site three days later.

Table 3.1. Summary of means and coefficients of variation (CV) of Call type I among nine male Piping Plovers in 1998¹⁾

Variable	Individuals									Average (N = 9)
	98-7M (n = 30)	98-8M (n = 20)	98-13M (n = 31)	98-15M (n = 30)	98-16M (n = 40)	98-17M (n = 30)	98-19M (n = 30)	98-29M (n = 40)	98-30M (n = 40)	
FP1	1927 ± 73.8 (3.8)	2339 ± 74.8 (3.2)	2329 ± 73.8 (3.2)	2168 ± 82.5 (3.8)	2059 ± 26.4 (1.3)	2190 ± 38.9 (1.8)	2027 ± 34.7 (1.7)	2233 ± 25.4 (1.1)	2133 ± 86.1 (4.0)	2156 ± 136.8 (6.3)
FP3	2323 ± 179.3 (7.7)	2510 ± 127.2 (5.1)	2483 ± 104.2 (4.2)	2482 ± 186.7 (7.5)	2203 ± 96.9 (4.4)	1933 ± 326.2 (16.9)	2523 ± 87.0 (3.4)	2311 ± 131.3 (5.7)	2332 ± 96.7 (4.1)	2344 ± 189.8 (8.1)
TP1	102 ± 6.8 (6.7)	109 ± 14.6 (13.4)	97 ± 3.9 (4.0)	77 ± 11.8 (15.3)	105 ± 3.8 (3.6)	116 ± 5.5 (4.8)	83 ± 3.6 (4.3)	85 ± 2.8 (3.2)	75 ± 5.1 (6.8)	94 ± 14.8 (15.7)
TIF	27 ± 4.0 (14.8)	26 ± 4.9 (18.6)	28 ± 4.0 (14.1)	20 ± 4.7 (23.0)	36 ± 4.5 (12.4)	31 ± 4.7 (15.3)	31 ± 2.4 (7.7)	31 ± 3.4 (10.7)	29 ± 3.2 (10.8)	28 ± 4.4 (15.3)
TP3	22 ± 2.2 (9.8)	23 ± 2.7 (11.4)	24 ± 1.6 (6.7)	22 ± 2.5 (11.3)	23 ± 2.0 (8.8)	23 ± 2.0 (8.6)	22 ± 1.8 (8.4)	22 ± 2.9 (13.1)	20 ± 2.1 (10.4)	22 ± 1.1 (5.0)
TC	169 ± 5.3 (3.1)	197 ± 11.2 (5.7)	164 ± 5.9 (3.6)	144 ± 17.7 (12.2)	179 ± 5.2 (2.9)	163 ± 5.7 (3.5)	163 ± 3.7 (2.3)	161 ± 3.5 (2.2)	149 ± 5.8 (3.9)	165 ± 15.6 (9.5)
TIC	72 ± 5.5 (7.6)	64 ± 5.2 (8.0)	105 ± 24.8 (23.7)	60 ± 17.7 (29.4)	65 ± 10.9 (16.7)	101 ± 26.0 (25.7)	37 ± 4.2 (11.5)	40 ± 6.1 (15.3)	63 ± 13.7 (21.7)	67 ± 23.3 (34.5)

¹⁾ Data are shown as mean ± SD (CV). Frequency variables were reported in Hz and temporal variables in msec; CV is reported as a percentage.

Table 3.2. Summary of CV - ratios¹⁾ and results of one-way ANOVAs with multiple comparisons for call type I

Variable	CV ratio	F-ratio ²⁾	Multiple comparisons ³⁾
FP1	2.4	145.8	(98-8M, 98-13M) (98-15M, 98-17M, 98-30M) (98-16M, 98-19M) (98-17M, 98-29M) (98-7M)
TP1	2.3	147.2	(98-7M, 98-13M, 98-16M) (98-8M, 98-16M) (98-15M, 98-30M) (98-19M, 98-29M) (98-17M)
TD	2.2	108.1	(98-7M, 98-13M, 98-17M) (98-13M, 98-17M) (98-13M, 98-17M, 98-29M) (98-13M, 98-17M, 98-19M, 98-29M) (98-15M, 98-30M)
TIC	1.9	78.5	(98-7M, 98-8M, 98-15M, 98-16M, 98-30M) (98-8M, 98-15M, 98-16M, 98-30M) (98-13M, 98-17M) (98-15M, 98-16M, 98-30M) (98-16M, 98-30M) (98-19M, 98-29M)
FP3	1.2	41.5	(98-7M, 98-16M, 98-29M, 98-30M) (98-8M, 98-13M, 98-15M, 98-19M) (98-8M, 98-13M, 98-15M) (98-13M, 98-15M) (98-16M, 98-29M, 98-30M)
TIF	1.1	39.7	(98-7M, 98-8M, 98-13M, 98-30M) (98-13M, 98-17M, 98-19M, 98-29M, 98-30M) (98-13M, 98-17M, 98-30M) (98-17M, 98-30M) (98-17M, 98-29M, 98-30M) (98-8M, 98-13M)
TP3	0.5	9.5	(98-7M, 98-8M, 98-15M, 98-16M, 98-17M, 98-19M, 98-9M) (98-7M, 98-8M, 98-15M, 98-16M, 98-17M, 98-29M) (98-8M, 98-13M, 98-15M, 98-16M, 98-17M, 98-29M) (98-13M, 98-16M, 98-17M) (98-15M, 98-16M, 98-17M) (98-15M, 98-16M, 98-17M, 98-29M) (98-16M, 98-17M) (98-30M)

¹⁾ CV - ratio = (CVa/CVw) (see methods).

²⁾ All F-ratios were highly significant ($p < 0.0001$; $df = 8, 282$).

³⁾ Simulation-based method was used for critical point calculation.

Table 3.3. Summary of data¹⁾, and results of one-way ANOVAs for comparisons of call type I between two periods for two males. The 98-16M calls of late date were recorded after eggs being predated, and 99-1M from lone male.

Variable	98-16M ²⁾		F	99-1M ³⁾		F
	May 30 (n = 40)	June 13 (n = 24)		June 17 (n = 30)	June 21 (n = 30)	
FP1	2059 ± 26.4	2084 ± 36.2	10.3 *** ⁴⁾	2176 ± 92.9	2147 ± 72.7	1.81
TP1	105 ± 4.4	104 ± 5.9	0.927	87 ± 5.8	99 ± 4.4	77.5 ***
TIF	36 ± 4.5	36 ± 5.7	0.003	27 ± 2.8	28.5 ± 4.0	2.53
TP3	22.7 ± 2.0	21.3 ± 1.9	7.84 **	24 ± 1.8	22.8 ± 2.1	12.7 ***
FP3	2203 ± 96.9	2282 ± 128.4	7.88 **	2479 ± 130.6	2429 ± 130.6	2.17
TD	180 ± 5.2	180 ± 8.0	0.008	153 ± 7.8	159 ± 4.8	11.4 **
TIC	65 ± 10.9	67 ± 13.2	0.412	70 ± 22.2	63 ± 17.4	1.60

** p < 0.01, *** p < 0.001.

¹⁾ Mean ± SD are shown.

²⁾ Paired on both dates; later recordings were made after nest was depredated.

³⁾ Unpaired on both dates.

⁴⁾ p values were corrected with a sequential Bonferroni tests.

However, the magnitude of differences were small compared with individual differences (Table 3. 1, 3. 2). Sequential effects appeared in FP1 of both individuals within a bout, but did not appear within 98-16M (Table 3. 4). Compared with the calls of 98-16M, those of 99-1M were more correlated in some variables, but it was not the same variables between bouts.

Vocal differences of call type I between aerial and ground calls

Sonagrams of aerial and ground versions of call type I from the same male are shown in Fig. 3. 3E - F. They are very similar in general structure but differ significantly on some quantitative measures (Table 3. 5).

INDIVIDUALITY IN CALL TYPES VI, VII, VIII

Sexual differences

Sexual differences were significant for all F - variables on each call type, and for four of six T - variables (Table 3. 6). The between-sex component of variance ranged from 0.8 to 52 % across variables; FP/VI (dominant frequency of call part of type VI) was highest. Means and CVs for all variables and call types for both sexes are presented in Table 3. 7. The frequency of female calls was higher. TP/VI and TC/VIII of females were significantly shorter while TP1/VII was longer than that of males.

Individual differences

Quantitative assessment of individuality is necessary because call type I is given only by males, and call types VI, VII, and VIII are much simpler so it is more difficult

Table 3.4. Summary of autocorrelation analysis for call type I within the same male on two dates. Significant lags at $\alpha = 0.5$ for lags 1 to 3 are shown.

Variable	98-16M				99-1M			
	May 30 (n = 40)		June 13 (n = 24)		June 17 (n = 30)		June 21 (n = 30)	
	Lag	t-statistic	Lag	t-statistic	Lag	t-statistic	Lag	t-statistic
FP1	1	4.50 ¹⁾			1	5.11	1	4.06
	2	2.66			2	2.79	2	2.18
					3	2.03		
TP1					1	2.91		
					2	2.71		
TIF							1	2.92
TP3								
FP3							1	2.11
TD								
TIC							1	3.57

¹⁾ p values were corrected with a sequential Bonferroni tests.

Table 3.5. Summary of data, and one-way ANOVAs comparing type I calls given in the ground and in the air

Variables	98-19M		F	99-3M ²⁾		F
	May 6 ¹⁾ (n = 33)	July 10 (n = 30)		May 19 ¹⁾ (n = 40)	May 19 (n = 35)	
FPI	2025 ± 33.8	2275 ± 52.3	517.8 *** ³⁾	2255 ± 66.8	2235 ± 67.0	1.713
TP1	83 ± 4.0	85 ± 5.1	1.921			
TIF	29 ± 2.9	31 ± 2.4	8.048 **			
TP3	24.0 ± 2.1	21.8 ± 1.8	19.05***			
FP3	2502 ± 85.1	2523 ± 87.0	0.921			
TD	172 ± 4.4	163 ± 3.7	90.39 ***			
TIC	74 ± 12.6	36 ± 4.2	242.5 ***			

* p < 0.01, *** p < 0.001.

¹⁾ Calls recorded on ground during copulation attempts; others were given in aerial display.

²⁾ Most variables were not measured because recordings were faint (Fig. 3G).

³⁾ p values were corrected with a sequential Bonferroni tests.

Table 3.6. Results of nested analyses of variance on F-variables variable (calls within individuals within sex)¹⁾

Individuals within sex/			Percent of variance		
Variable	MS _S /MS _I	MS _S /MS _C	Sex	Individual	Call
Frequency attributes					
FP/VI	1148.60***	48.23***	52.2	33.6	14.2
FP2/VII	35.10***	8.94***	20.0	42.5	37.5
FP1/VII	44.95***	14.60***	17.4	54.5	28.1
FC/ VIII	176.45***	80.73***	8.8	73.0	18.3
Temporal attributes					
TP/ VI	119.72***	22.67***	13.5	45.0	41.6
TP2/ VII	0.32	12.15***	8.5	56.2	35.3
TIP/VII	0.34	11.45***	8.3	54.9	36.8
TC/VIII	147.56***	88.07***	5.3	77.0	17.7
TP1/VII	10.03**	6.19***	4.3	40.7	55.0
TIC/VIII	20.31***	17.54***	0.8	44.9	54.3

** p < 0.01; *** p < 0.001.

¹⁾ MS = mean square; S = sex; I = individual; C = call.

Table 3.7. Summary of data on variation in selected calls at individual and population levels

Variable	Male				Female				Totals		
	Mean	mean ¹⁾ CV _w	CV _A ²⁾	ratio ³⁾	Mean	mean CV _w	CV _A	ratio	Mean	CV	N ⁴⁾
Frequency attributes											
FP/VI	2591	1.8	2.8	1.5	2730	1.8	3.1	1.7	2661	4.3	30 (600)
FP1/ VII	2254	7.5	12.9	1.7	2506	4.7	9.8	2.1	2380	13.8	14 (98)
FP2/ VII	1941	9.4	10.0	1.0	2154	4.9	9.6	2.0	2048	13.3	14 (98)
FC/ VIII	2547	2.3	3.5	1.5	2631	2.0	5.9	3.0	2589	5.5	20 (400)
Temporal attributes											
TP/ VI	172	13.3	16.1	1.2	150	17.0	17.2	1.0	161	23.3	30 (600)
TP1/ VII	82	11.0	12.0	1.1	88	11.1	8.5	0.8	85	15.2	14 (98)
TIP/ VII	66	27.9	35.7	1.2	68	27.9	28.4	1.1	67	37.5	14 (98)
TP2/ VII	80	33.2	59.6	1.8	84	29.7	32.2	1.1	82	55.0	14 (98)
TC/ VIII	68	6.2	14.6	2.4	63	7.6	15.4	2.0	66	16.4	20 (400)
TIC/ VIII	346	2.4	25.9	10.8	386	2.1	19.9	9.5	366	32.6	20 (400)

F - variables are in Hz and T - variables in msec.

¹⁾ CV_w = within - individual coefficients of variation.²⁾ CV_A = between - individual coefficients of variation.³⁾ ratio = (CV_A / mean CV_w).⁴⁾ Sample sizes are shown for : individuals (calls).

to identify the sex and individuality of calling birds. Call type VI was the most complex of these calls (Fig. 3. 4). However, it did not occur frequently, varied within individuals, and was difficult to record from many birds.

Significant variation among individuals within sexes occurred in all of F - and T - attributes: the component of variation ranged from 34 to 77 % across variables in the nested GLMs (Table 3. 6). In addition, the CV - ratio showed that call individuality was strong in each variable except TP1/VII of female calls (Table 3. 7). FC/VIII of female calls and TIC/VIII were stereotyped (CV - ratios, 3.0 - 10.8). T - variables on call type VI, VII and FP2/VII of male calls were less stereotyped (CV - ratios, 0.8 - 1.8). In addition, sequential effects on the calls of call type VIII appeared for all variables (Table 3. 8).

Variation of call types VI, VII, and VIII between breeding stages

Call variables of type VI from the same individuals within breeding stages are compared in Table 3. 9. Significant differences occurred for FP in five of 14 individuals and for TP in four individuals. FP showed an increasing trend between pre-hatching and the day of hatching, then decreased. There were no differences in comparisons of pre- and post-hatching days. Significant differences were also found for each variable of call type VIII in some individuals in Table 3. 10. It shows that vocal stability of each individual could be kept by combining these variables. Call type VII showed large differences between hatching period and post-hatching days despite small sample sizes (Table 3. 11). F - variables and two T - variables, TIP and TP2, varied more within the hatching period than post-hatching stage.

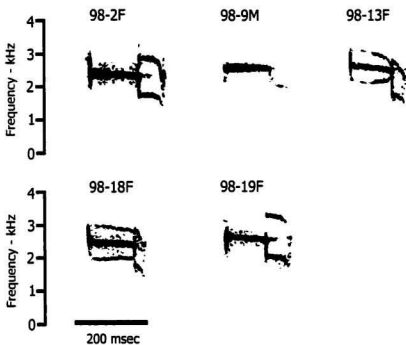


Figure 3.4. Sonograms of call type VI recorded in 1998 showing differences between individuals. 98-9M emitted unique metallic-sounding.

Table 3.8. Results of autocorrelation of call type VIII. Significant lags at $\alpha = 0.5$ from lags 1 through 3 were indicated.

Variables	98-19M (n = 72)		98-18M (n = 63)	
	Lag	t-statistic	Lag	t-statistic
FC	1	2.41 ¹⁾	1	2.85
TC	1	2.04	1	6.57
			2	3.96
			3	3.22
TIC	1	3.79	1	4.81
	2	2.53	2	2.74

¹⁾ p values were corrected with a sequential Bonferroni tests.

Table 3.9. Mean \pm SD, and results of Mann-Whitney tests comparing vocal variables of call types VI in 1998. Calls were recorded from the same individuals between breeding stages: 1 - pre-hatching, 2 - day of hatching, and 3 - post-hatching.

Individual	FP (Hz)			Mann-Whitney U	TP (msec)			Mann-Whitney U
	1	2	3		1	2	3	
98-3F	2780	2787		205	156	162		187.5
(n = 21, 21) ¹⁾	± 30.0	± 47.4			± 16.0	± 22.2		
98-3M	2442	2514		15.5 ^{***2)}	172	176		49
(n = 10, 10)	± 59.4	± 50.3			± 23.4	± 15.2		
98-13M	2448	2631		0 ^{**}	132	176		8.5 ^{**}
(n = 12, 8)	± 46.2	± 37.0			± 22.8	± 38.6		
98-14F	2851	2779		140.5 ^{**}	153	143		253.5
(n = 16, 39)	± 107.6	± 95.8			± 70.4	± 23.7		
98-14M	2644	2626		345	171	151		169 ^{**}
(n = 23, 40)	± 47.3	± 46.0			± 18.4	± 19.2		
98-15M	2499	2599		27 ^{**}	136	127		163.5
(n = 22, 21)	± 44.5	± 52.1			± 20.4	± 22.2		
98-19M	2531	2675		0 ^{***}	165	167		71.5
(n = 8, 18)	± 29.6	± 48.1			± 22.3	± 17.0		
98-8F		2648	2623	79		148	155	122.5
(n = 8, 35)		± 29.6	± 29.0			± 20.0	± 25.6	
98-8M		2657	2635	44.5		152	123	12 ^{**}
(n = 14, 10)		± 27.6	± 39.8			± 18.5	± 10.2	
98-22M		2536	2523	74		174	168	71.5
(n = 13, 14)		± 27.6	± 45.5			± 34.4	± 22.1	
98-5M	2486		2508	41.5	130		126	66.5
(n = 23, 7)	± 30.1		± 17.0		± 15.6		± 11.6	
98-7F	2753		2753	24.5	164		176	16.5
(n = 7, 7)	± 27.0		± 18.8		± 20.6		± 12.6	
98-7M	2695		2700	23.0	187		165	20.5
(n = 7, 7)	± 37.3		± 40.1		± 26.7		± 20.0	
98-18F	2627		2660	34.5	163		111	0 ^{***}
(n = 10, 12)	± 66.4		± 35.1		± 12.3		± 20.6	

^{*} $p < 0.05$, ^{**} $p < 0.01$, ^{***} $p < 0.001$.

¹⁾ n (calls in order of stages).

²⁾ p values were corrected with a sequential Bonferroni tests.

Table 3.10. Mean \pm SD, and results of Mann-Whitney tests comparing vocal variables of call type VIII in 1998. Calls were recorded from the same individuals: early and late in the stage of post-hatching.

Individual	FC (Hz)		Mann-Whitney U	TC (msec)		Mann-Whitney U	TIC (msec)		Mann-Whitney U
	Early	Late		Early	Late		Early	Late	
98-18M (n = 14, 13) ¹⁾	2548 \pm 34.1	2500 \pm 167.7	72	66 \pm 5.9	73 \pm 6.2	27**	368 \pm 144.9	299 \pm 165.2	54
98-21M (n = 24, 19)	2478 \pm 23.9	2547 \pm 10.5	10.5*** ²⁾	68 \pm 3.4	63 \pm 3.9	50.5***	401 \pm 152.9	349 \pm 181.1	175.5
98-22M (n = 44, 36)	2506 \pm 25.3	2513 \pm 58.2	739	65 \pm 3.1	67 \pm 6.3	715	266 \pm 30.2	442 \pm 77.0	0***
98-24M (n = 18, 16)	2642 \pm 51.2	2760 \pm 38.1	8***	63 \pm 5.5	66 \pm 4.1	70.5*	473 \pm 239.4	458 \pm 245.7	144
98-26F (n = 43, 26)	2736 \pm 46.7	2725 \pm 55.4	454	57 \pm 3.1	59 \pm 3.2	408	470 \pm 118.4	428 \pm 80.2	367

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

¹⁾ n (calls in order of early, late).

²⁾ p values were corrected with a sequential Bonferroni tests.

CLASSIFICATION TREE ANALYSIS

Two classification trees for males were constructed. One used six variables on call type I with 291 calls for classifying nine males recorded in 1998. The other used five variables on call types VI and VIII (132 calls, 11 males). A classification tree for seven females was constructed with five variables on call types VI and VIII (140 calls). Call type VII was excluded from analysis because of high variation between breeding stages (Table 3. 11). Non-uniform node was produced to show the importance of the parent splits by the perpendicular length of the branches. In addition, pruning process was successively performed to get optimal trees for each group.

A classification tree for call type I is shown in Fig. 3. 5. The pruned tree fitted for producing nine terminal nodes was first split by a value of 92.5 msec for TP1 at the root node. If it was less than 92.5 msec, TIC was selected as a second decision rule, followed by FP1 and TIF on the left branch. FP1 classified 98-19M calls and 98-29M calls, and TIF classified 98-15M and 98-30M. On the right branch, FP1 was chosen for the second node, FP1 and FP3 for the third node, and TC for the fourth. Boxplots on the calls of nine individuals are given in Fig. 3. 6. The horizontal lines on the graphs showed clear cutpoints used as decision rules in the tree. For example, the initial cutpoint of 92.5 msec of TP1 in the tree properly classified individuals into two separate groups based on the maximal deviance of 441.0. The second cutpoint of 48.5 msec on TIC separated males 98-19M and 98-29M from 98-15M and 98-30 in the left branch; a cutpoint of 2112.5 Hz for FP1 separated males 98-7M and 98-16M from other males in the right branch.

Call types VI and VIII were used together for growing trees for both sexes (Figs.

Table 3.11. Summary of mean \pm SD showing variations of call type VII from the same individuals between breeding stages in 1998: 2 - hatching period and 3 - post-hatching.

Individual	Variable									
	FP1		FP2		TP1		TIP		TP2	
	2 ¹⁾	3	2	3	2	3	2	3	2	3
98-1F (n = 6, 6) ²⁾	2227 ± 509.9	2600 ± 20.8	1932 ± 381.3	2134 ± 264.9	114 ± 12.3	118 ± 19.4	55 ± 44.2	79 ± 11.3	109 ± 47.2	79 ± 30.1
98-22M (n = 4, 4)	2323 ± 139.1	2465 ± 34	1914 ± 180.5	2125 ± 48.4	92 ± 17.0	80 3.0	53 ± 26.3	90 ± 9.4	123 ± 86.3	66 11.2
98-23 (n = 4, 4)	2529 ± 20.9	2508 ± 24.0	2205 ± 19.6	2162 ± 28.9	86 ± 1.2	82 ± 7.1	190 ± 36.1	75 ± 3.1	110 ± 48.0	83 ± 4.4

F₁- variables were reported in Hz and T- variables in msec.

¹⁾ From hatching day until after one week

²⁾ n (calls in order of stages)

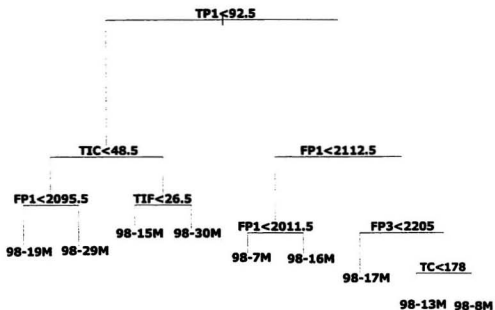


Figure 3.5. Classification tree of call type I recorded in 1998 to predict males from call variables.

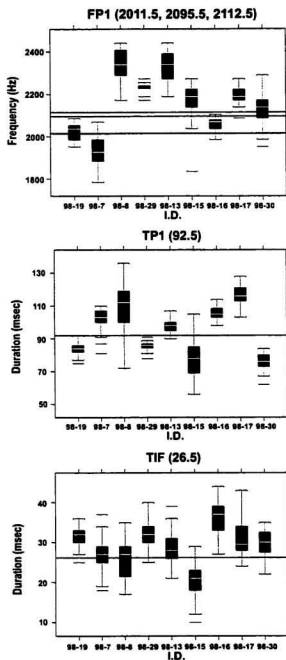


Figure 3.6. Boxplots of call type I variables showing data distributions for each individual. Horizontal lines were used for classification of individuals on the classification tree. The box displays boundaries of upper and lower quartiles; medians are represented by white horizontal lines.

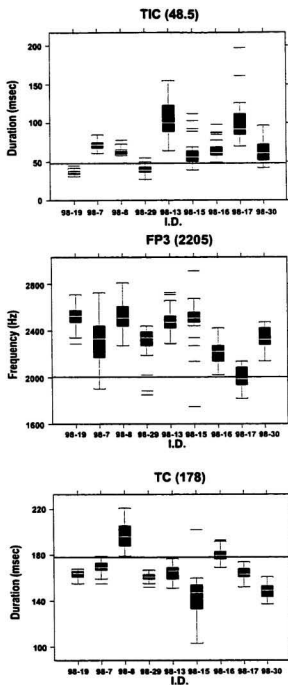


Figure 3.6. (Continued).

3. 7, 3. 9). Boxplots for these call types are given according to each tree of females and males in Figs. 3. 8 and 3. 10. The trees were divided into subgroups by 2642.5 Hz on FC for call type VIII for females, which had maximal deviance of 248.6 and by 80.5 msec on TC of call type VIII for males, which had a maximal deviance of 470.1. The group of females at the second node was subdivided by FC of call type VIII (2449 Hz for left branch, 2861.5 Hz for right). In contrast, the tree of males used TP for call type VI (176 msec) to classify calls of 98-14M and 98-1M, and FP of call type VI (2516.5Hz) to separate males 98-5M and 98-22M from six others. The remaining individuals were classified according to relatively homogeneous groups at each node. The residual mean deviance and misclassification error rate for the above trees are shown in Table 3. 12.

The classification tree of call types VI and VIII was applied to the calls recorded from a banded male in 1999 (Fig. 3. 9). Information on the banded males in 1998 and 1999 is summarized in Table 3. 13. Calls of 99-2M recorded in 1999 were correctly traced to 98-4M based on decision rules of the tree, in which 98-4M was separated from 98-1M (another male banded in 1998) at the root node using TC of call type VIII: This variable shows high individuality (Table 3. 7).

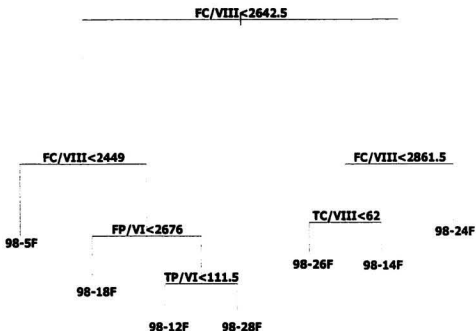


Figure 3.7. Classification tree of call types VI, VIII from females recorded in 1998 to classify individuals from the call variables.

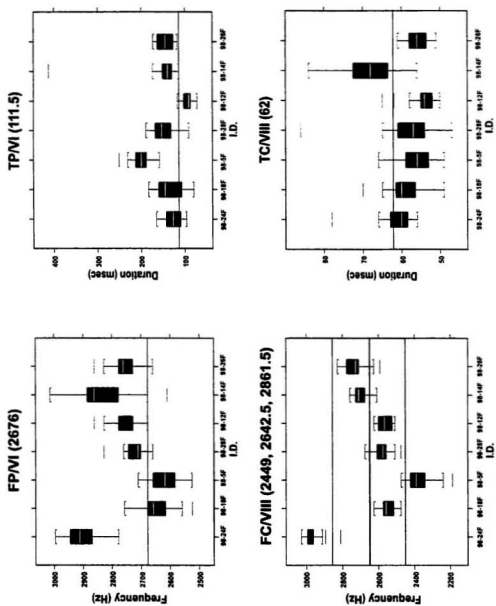


Figure 3.8. Boxplots of call type VI, VIII variables of females.

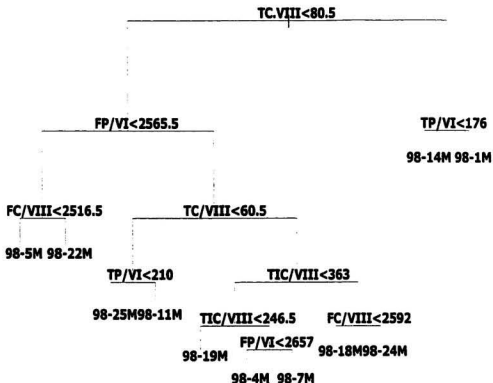


Figure 3.9. Classification tree of call types VI, VIII from males recorded in 1998 to classify individuals from the call variables.

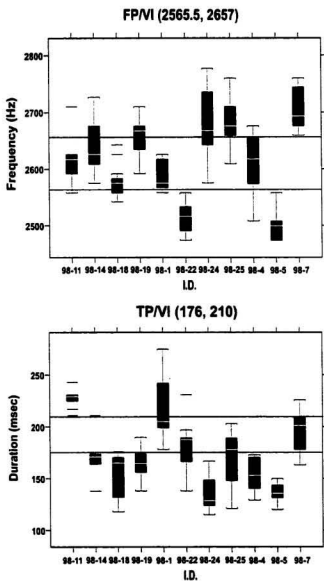


Figure 3.10. Boxplots of call type VI variables showing the data distribution of males.

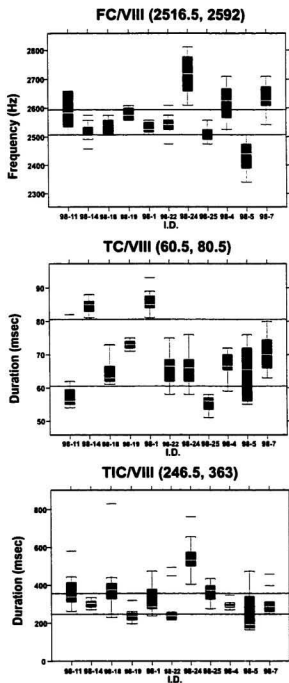


Figure 3.10. Boxplots of call type VIII variables showing the data distribution of males.

Table 3.12. Summary of results from three different classification trees on both sexes

Sex	Call type used in tree construction	No. of terminal nodes	Residual mean deviance	Misclassification error rate
M	I	9	0.7672	32 / 291
M	VI, VIII	11	1.144	24 / 132
F	VI, VIII	7	0.8178	16 / 140

Table 3.13. Comparisons of the calls of banded males in 1998 and banded male that returned in 1999.

Variable	98-1M	98-4M	99-2M
Call type VI			
FP	2597 \pm 31.3 (n = 36)	2613 \pm 50.0 (n = 12)	2653 \pm 39.3 (n = 22)
TP	214 \pm 29.2 (n = 36)	154 \pm 15.95 (n = 12)	187 \pm 21.6 (n = 22)
Call type VIII			
FC	2551 \pm 62.4 (n = 47)	2596 \pm 76.9 (n = 14)	2699 \pm 53.0 (n = 18)
TC	81 \pm 5.8 (n = 47)	67 \pm 3.4 (n = 14)	69 \pm 7.7 (n = 18)
TIC	275 \pm 59 (n = 47)	294 \pm 20.8 (n = 14)	297 \pm 49.2 (n = 17)

p < 0.05, ** p < 0.01.

Values are means \pm SD.

DISCUSSION

Individuality in call type I

Males were individually identifiable by sonagrams and statistical analysis. Call type I was complex and stereotyped within individuals and varied greatly between individuals. This call type has three useful attributes as a management tool (Gilbert and McGregor 1994). (1) First, it could be recorded readily from newly arrived territorial males engaged in courtship or territorial behaviour, from renesting males, and from males attending chicks. The call is loud and is given in bouts over periods lasting from a few minutes to several hours; sometimes it was given several times per day. (2) Individualistic features were visually apparent based on inspection of sonagrams, and were detected in statistical analysis. Multiple comparisons revealed significant individual differences in the high CV – ratio, especially for variables of FPI, TP1, and TD (Table 3. 2). In addition, these variables were important in constructing a classification tree. (3) Only minor differences were detected between samples from different time periods. Indeed, the calls were similar even between aerial and ground performances (Fig. 3. 3). It is likely that this call type is constant throughout life, because the call comparisons of 98-19M in this study covered a vocally inactive period of about two months. Furthermore, shorebirds are other non-passerine taxa likely having non-learned vocalizations (Siegel et al. 1965; Nottebohm and Nottebohm 1971; Miller 1986, 1992; Abs and Jeismann 1988; Kroodsma and Konishi 1991; Bretagnolle 1996). Baptista (1996) argued that even birds, which can learn songs or calls, might have genetically determined temporal, frequency, and tonal characteristics.

Quantitative measurements of call variables between periods revealed some statistical differences, possibly due to changes of internal state such as temporary fatigue from a series of long performances. On the day of June 19, 99-1M gave aerial displays eight times from 10:00 to 15:00, with displays lasting 30 sec to 1.5 hr, and only with short breaks. Cairns (1997) reported that the calls in aerial display might be given during the night. However, the mean difference of the variables between two dates was much smaller than that of the variables between different males. Furthermore, the boxplots of call type I showed how the males were clearly separated from each other with little misclassification (Fig. 3. 6).

Individuality in call types VI, VII, and VIII

Results from the combined variables of call type VI and VIII showed that individuals could be identified using quantitative methods. These call types were used in contexts of alarm so could be readily elicited from the onset of egg-laying to rearing chicks for call type VI, and usually from one week after hatching to fledging for call type VIII. In addition, call type VI is loud and given repetitively, so large samples of high quality can be obtained.

Highly significant differences among individuals were found in all variables of both call types VI and VIII. Variables TC and TIC on call type VIII showed a high CV - ratio in males and females, as did FC on call type VIII in females. Therefore, these variables are useful for individual classification. However, there are difficulties in identifying individuals due to seasonal and yearly variation. Significant differences within individuals appeared in seasonal comparisons for FP on call type VI and TP on call type VIII. Inter-annual differences were found for the banded bird for variables

on call type VI, and for FC on call type VIII. Many causes may underlie variations within individuals. One possible cause is changes of motivational state (Morton 1982). For instance, the frequency of call type VI increased on the day of hatching, which is the most sensitive to predators, then declined. The increased frequency reflects high chick vulnerability. Thomas et al. (1998) showed that about two third of lost chicks occurred within three days after eggs hatched. Another cause is variability in recording conditions (e.g. distances, wind). Lengagne et al. (1999) showed that the increase in windy conditions led to a diminution of the signal-to-noise ratio, which considerably influences attenuation of the signals. In particular, call type VIII, which are rapidly repeated calls of high frequency, may affect the recordings (Wiley and Richards 1982). A third possibility is that variations were caused by sequence effects (Table 3. 4, 3. 8). The results showed that the partial recording of the series would have different distribution of the data.

Diverse techniques for identifying individuals by voice have been suggested in non-passerines even if they have seasonal and inter-annual differences in some variables. Abs and Jeismann (1988) and Galeotti et al. (1993) used multiple variables, and Otter (1996) distinguished individuals with use of a low variant frequency. Some attempts to identify individuals have failed due to high variability (e.g. chatter calls of adult Bald Eagles, *Haliaeetus leucocephalus*; Eakle et al. 1989).

Call type VII is used as a contact call between mates, between parents and chicks, and among migrating birds. The call consists of two parts. Individual identification using this call type was difficult because it varied between breeding stages and showed low individuality within the hatching period. However, it might be possible

to identify individuals by combining relatively invariant variables, such as FPI, with those of call type VI and VIII if being recorded within the same stage.

The use of Piping Plover vocalizations as a census tool

McGregor and Byle (1992) suggested that there is an upper limit on how many individuals can be identified by voice, and pointed out that most studies have used less than 20 individuals. If applied to male vocalizations of Piping Plovers, the technique using visual assessment and a classification tree has advantages and disadvantages. Call type I is complex and has many individually distinctive features. However, the best period for recording the call is brief: pre-pairing and early pairing. Another disadvantage is that males may wander more before establishing a territory. In addition to call type I, quantitative comparisons of combined call types VI and VIII will improve accuracy of identifying males. Besides, call types VII and IV will possibly be used in combination with call types VI and VIII. Call type IV was not used in this study because of small sample sizes. However, it is emitted frequently during aerial display, and preliminary analysis showed that it might be individually distinctive.

Female individuality was assessed quantitatively using call types VI and VIII. Like males, the inclusion of other individualistic variables (e.g. frequency attributes of call type VII) will improve classification trees. However, this method will have a restriction for sample sizes because of individual variation. To reduce such variation probably caused by the motivational state and recording quality, recording of call type VI around the time of hatching should be excluded, and standard recording distances, for example, about 10 m away from the caller, used especially for call type VIII.

Classification trees have been applied to identify individual animals based on fatty acid signatures in milk (Smith et al. 1997; Iverson et al. 1997). Smith et al. (1997) reported that 44 of 51 seals were correctly classified by this method, and when the tree developed from 1990 data was applied to 1993 data, misclassification rate was 5/15. Considering the large number of variables (> 60), they developed an effective tool for the species having many subjects and complicated data sets. In this study, adequate number of terminal nodes in each tree was larger than that of the trees grown by the pruning process, 12 for the classification tree of call type I, 17 for male of call types VI and VIII, and 8 - 9 for the female tree. This is because the lower node numbers from pruned trees leads to higher misclassification rate.

Therefore, my results suggest several possible methods to reduce the misclassification rate. First, other variables could be added to the classification tree. Secondly, shrinking process, which is another method to reduce the number of effective nodes, could be used because it will improve the accuracy better than pruning process (Clark and Pregibon 1992). Third, each mean value of two or three calls could be used if a large number of calls are recorded.

CHAPTER 4. CONCLUSIONS

Vocal repertoire

The vocal repertoire of Piping Plovers was classified into ten distinct call types for adults and three for chicks. All except call type I were used by both males and females. Similar structural properties with the functions conveyed in the vocal signals appeared among *Charadrius* species. Call type I was mainly accompanied by advertisement flights, which were performed by newly arrived territorial males, by reneesting males, and by males attending chicks. Observations on behaviours of mated and unmated males suggest that call type I has broad sexual and aggressive-territorial functions. This call showed high structural similarity with Ringed, Little Ringed, and Semipalmated Plovers: a tripartite structure and sequence. However, the fine structures of rhythmically repeated calls differed among these species.

Call types II, III, and VII were used as a contact call between mates or parents and chicks. These call types consist of a brief and soft call or two call parts, which are adequately adapted for short-range communications. Call types IV, VI, VIII, IX, and X were attributed to alarm calls, which is a major functional category of birds inhabiting open environments. Call type IV, VIII, and X were used more with relation to territory defense, and often presented in combined form (call type IV and X). The rising whistle shape and trill like calls were common among *Charadrius* species to threaten or warn the predators or conspecific birds. Call type VIII is a kind of 'chatters' type call used in response to terrestrial predators, while call type IX is 'whistles' type call used in response to aerial predators, which are extensive phenomenon in many birds and mammals. The observations of the behaviour of the

Piping Plover suggest that the call types result from response urgency rather than predator type. However, it needs to be tested for confirming the function of the call types. Call type VI was used in relation to predator distraction and was loud enough to arouse potential predators' attention. In addition, whistle calls, call type IV of adults and call types I and II of chicks, form an adapted characteristic to the open-country environments because of a low localizability. On the contrary, chatter calls of call type VIII of adults and wide band trill calls of call type III of chicks enhance the opportunity to locate position.

Individuality

The results of visual analysis of call type I showed high individuality: the call was complex, stereotyped within individuals, varied greatly among individuals, and showed vocal constancy between different periods. The assessment of quantitative analysis was significantly different among individuals, and different between two periods in some variables. However, the analysis of the data distribution on classification trees showed that the males were clearly separated from each other with few instances of misclassification. Visual identification based on the call types VI, VII, and VIII was not successful. However, quantitative analyses showed that the calls were significantly different among individuals within sexes in selected call variables and between sexes except for two variables of call type VII. The frequency of females was higher than that of males and the duration of call or call part was significantly shorter in call types VI and VIII. Call type VII showed large differences between hatching and post-hatching days, and varied greatly within hatching days. Classification trees constructed based on call type I for male and two call types (VI

and VIII) for males and females were effective for classifying and re-identifying individuals. One male banded in 1998 was successfully re-identified using this tree in 1999.

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Appendix A. Summary of information on the study animals. (From Thomas et al. 1998, 1999)

Nest location	Nest Number	ID	1 Egg Laying Date	4 Egg Laying Date	Hatching Date	Fledged Date	Comments
Cavendish Sandspit	CS1-a	98-1	12 May	17 May	12 June	02 July	Adult male banded
	CS2-a	98-2	N/A	17 May	11 June	01 July	
	CS3-a	98-3	N/A	15 May	10 June	30 June	
	CS4-a	98-4	12 May	17 May	11 June	02 July	Adult male banded
	CS5-a	98-5	N/A	15 May	11 June	01 July	
	CS6-a	98-6	N/A	15 May			Egg buried
	CS7-a	98-7	13 May	19 May	14 June	04 July	
	CS8	98-8	02 June	09 June	04 July	24 July	
	CS9	98-9	04 June	10 June	05 July	25 July	
	CS10	98-10	07 June	12 June	07 July		
	CS11	98-11	12 June	17 June	14 July	03 August	
Rustico Causeway	RC1-a	98-12	N/A	14 May	08 June	29 June	Adult female banded
	RC2-a	98-13	N/A	16 May	11 June	02 July	
	RC3-a	98-14	13 May	20 May	15 June	06 July	
	RC4-a	98-15	21 May	27 May	22 June	12 July	Adult female banded Nest lost
	RC5-a	98-16	05 June				
	RC6-a	98-17	N/A	10 June			Nest lost
Covehead Beach	CH1-a	98-18	08 May	13 May	07 June	28 June	

Appendix A. Continued.

Nest location	Nest Number	ID	1 Egg Laying Date	4 Egg Laying Date	Hatching Date	Fledged Date	Comments
Covehead beach	CH2-a	98-19	N/A	16 May	10 June	30 June	Adult female banded
	CH4	98-20	30 May	04 June	29 June	19 July	
North Rustico Beach	NR1	98-21	N/A	19 June	15 June	05 August	3 eggs laid
Rustico Island Beach	RIS1-a	98-22	N/A	27 May	22 June	14 July	
Blooming Point	BP1-a	98-23	N/A	18 May*	14 June	04 July	
	BP2	98-24	25 June	29 June	25 July	15 August	
Greenwich Beach	GR1-a	98-25	N/A	15 June*	03 July		4 egg missing
Savage Harbour	SA	98-26	N/A	24 May*	20 June	12 July	
St. Peter's Harbour	SP	98-27	N/A	28 May*	23 June	15 July	
Darnley Point	Dar	98-28	N/A	5 June*	2 July	21 July	
Cavendish Sandspit		98-29					Territorial behaviour without nest
Rustico Causeway		98-30					Territorial behaviour without nest
Cavendish Sandspit	Cs2l	99-1	23 June				Abandoned
	Cs5b	99-2	29 May	3 June	30 June	20 July	Adult male banded in 1998

Appendix A. Continued.

Nest location	Nest Number	ID	1 Egg Laying Date	4 Egg Laying Date	Hatching Date	Fledged Date	Comments
Covehead Beach	CH2a	99-3	11 May				Nest abandoned
	CH2b	99-4					Territorial behaviour without nest
Rustico Causeway		99-05					Territorial behaviour without nest

* The date laying four eggs was inferred by egg(s) found during visiting nests.

Appendix B. Quantitative analysis of call type VI of Piping Plovers. Data are shown as mean \pm SD. Frequency variable is reported in Hz and temporal variable in msec.

Individuals	Number of calls	Dominant Frequency of call part	Duration of call part
Bp1f	8	2781 \pm 87	113 \pm 10
Bp1m	37	2577 \pm 29	17 \pm 4
Bp2f	30	2893 \pm 35	132 \pm 20
Bp2m	36	2701 \pm 47	14 \pm 19
Cb3f	29	2678 \pm 27	111 \pm 13
Cb3m	5	2548 \pm 80	116 \pm 26
Ch1f	22	2645 \pm 53	135 \pm 31
Ch1m	25	2566 \pm 57	16 \pm 26
Ch2f	75	2742 \pm 81	181 \pm 24
Ch2m	26	2630 \pm 80	167 \pm 18
Ch4f	9	2584 \pm 50	131 \pm 18
Ch4m	19	2561 \pm 52	157 \pm 17
Cs10m	42	2574 \pm 17	193 \pm 24
Cs11f	26	2810 \pm 44	144 \pm 32
Cs11m	36	2615 \pm 35	216 \pm 29
Cs1f	16	2569 \pm 40	199 \pm 30
Cs1m	40	2598 \pm 29	214 \pm 30
Cs2f	5	2672 \pm 30	161 \pm 9
Cs2m	32	2649 \pm 62	165 \pm 22
Cs3f	50	2784 \pm 38	159 \pm 18
Cs3m	44	2464 \pm 57	167 \pm 19

Appendix B. Continued.

Individuals	Number of calls	Dominant Frequency of call part	Duration of call part
Cs4f	12	2628 \pm 30	153 \pm 22
Cs4m	12	2613 \pm 50	154 \pm 15
Cs5f	29	2620 \pm 48	198 \pm 18
Cs5m	30	2491 \pm 28	130 \pm 15
Cs6f	51	2678 \pm 45	141 \pm 16
Cs6m	17	2541 \pm 22	174 \pm 13
Cs7f	21	2736 \pm 37	171 \pm 20
Cs7m	40	2687 \pm 42	181 \pm 26
Cs8f	45	2627 \pm 30	153 \pm 33
Cs8m	25	2643 \pm 41	142 \pm 23
Cs9f	23	2769 \pm 60	136 \pm 29
Cs9m	14	2590 \pm 35	175 \pm 22
Darf	22	2718 \pm 39	147 \pm 28
Grf	13	2692 \pm 30	16 \pm 19
Grm	23	2680 \pm 38	173 \pm 28
Nrf	10	2696 \pm 40	154 \pm 34
Nrm	10	2469 \pm 48	162 \pm 13
Rc1f	27	2755 \pm 43	97 \pm 13
Rc1m	12	2482 \pm 31	11 \pm 7
Rc2f	44	2612 \pm 44	145 \pm 25

Appendix B. Continued.

Individuals	Number of calls	Dominant Frequency of call part	Duration of call part
Rc2m	20	2522 \pm 100	15 \pm 37
Rc3f	55	2800 \pm 103	147 \pm 42
Rc3m	63	2632 \pm 46	159 \pm 21
Rc4f	21	2616 \pm 48	155 \pm 19
Rc4m	43	2548 \pm 69	132 \pm 22
Rsf	9	2807 \pm 55	136 \pm 18
Rsm	29	2528 \pm 36	173 \pm 28
Saf	23	2759 \pm 49	143 \pm 19
Sam	40	2710 \pm 68	136 \pm 24
Spf	39	2641 \pm 31	124 \pm 16
Total	1434	2653 \pm 108	157 \pm 35

Appendix C. Quantitative analysis of call type VII of Piping Plovers. Data are shown as mean \pm SD. Frequency variables are reported in Hz and temporal variables in msec.

Individuals	Number of calls	Dominant frequency of first call part	Duration of first call part	Interval between call parts	Dominant frequency of second call part	Duration of second call part
Bp1m	4	2529 \pm 21	86 \pm 1	190 \pm 36	2205 \pm 20	110 \pm 48
Bp2f	7	2734 \pm 57	89 \pm 1	84 \pm 18	2234 \pm 61	80 \pm 28
Bp2m	4	2718 \pm 133	88 \pm 20	73 \pm 18	2239 \pm 259	78 \pm 19
Cb3m	12	2006 \pm 235	65 \pm 10	60 \pm 15	1807 \pm 132	61 \pm 41
Ch1m	2	2634 \pm 35	101 \pm 7	73 \pm 0	2231 \pm 12	60 \pm 15
Ch2m	5	2619 \pm 117	75 \pm 4	69 \pm 4	2350 \pm 119	56 \pm 2
Ch4f	2	2374 \pm 71	74 \pm 1	103 \pm 8	2054 \pm 23	63 \pm 11
Ch4m	2	2466 \pm 12	98 \pm 25	84 \pm 4	2407 \pm 24	72 \pm 1
Cs10m	30	2566 \pm 52	98 \pm 37	98 \pm 16	2127 \pm 177	51 \pm 18
Cs11f	21	2682 \pm 145	78 \pm 6	80 \pm 10	2328 \pm 94	131 \pm 29
Cs11m	16	2603 \pm 35	86 \pm 6	82 \pm 6	2258 \pm 65	74 \pm 18
Cs1f	13	2342 \pm 349	105 \pm 12	81 \pm 10	2002 \pm 259	97 \pm 34
Cs3m	45	2294 \pm 226	86 \pm 1	64 \pm 23	2071 \pm 196	83 \pm 17
Cs5m	3	2272 \pm 236	75 \pm 2	73 \pm 8	1846 \pm 171	65 \pm 20
Cs7f	10	2629 \pm 45	92 \pm 5	94 \pm 18	2269 \pm 41	70 \pm 12

Appendix C. Continued.

Individuals	Number of calls	Call type VII				
		Dominant frequency of first call part	Duration of first call part	Interval between call parts	Dominant frequency of second call part	Duration of second call part
Cs7m	3	2654 ± 25	96 ± 17	108 ± 46	2312 ± 79	75 ± 20
Cs8f	6	2572 ± 53	76 ± 5	72 ± 9	2149 ± 122	87 ± 32
Cs9f	32	2714 ± 163	84 ± 7	65 ± 6	2316 ± 90	55 ± 14
Cs9m	8	1967 ± 194	78 ± 6	49 ± 18	1860 ± 256	61 ± 15
Darf	2	2416 ± 416	107 ± 19	107 ± 19	2197 ± 392	168 ± 6
Nrf	11	2461 ± 98	94 ± 17	72 ± 20	2176 ± 127	118 ± 52
Nrm	24	2469 ± 46	98 ± 14	96 ± 14	2094 ± 95	166 ± 65
Rc1f	2	2719 ± 12	91 ± 0	68 ± 9	1784 ± 143	64 ± 12
Rc1m	4	1578 ± 247	77 ± 3	39 ± 4	1212 ± 83	68 ± 22
Rc2m	7	2212 ± 500	79 ± 9	58 ± 27	1806 ± 480	48 ± 6
Rc3m	6	2303 ± 233	83 ± 10	57 ± 29	2039 ± 177	59 ± 12
Rc4f	15	2079 ± 240	84 ± 14	34 ± 30	1799 ± 193	86 ± 28
Rsm	4	2323 ± 139	92 ± 17	53 ± 26	1915 ± 181	123 ± 86
Saf	9	2618 ± 42	89 ± 5	63 ± 8	2257 ± 70	65 ± 31
Sam	1	2491	82	57	2087	69

Appendix C. Continued.

Individuals	Number of calls	Call type VII				
		Dominant frequency of first call part	Duration of first call part	Interval between call parts	Dominant frequency of second call part	Duration of second call part
Spf	1	2474	80	90	2138	113
Total	311	2447 \pm 294	87 \pm 17	74 \pm 28	2110 \pm 251	45 \pm 45

Appendix D. Quantitative analysis of call type VIII of Piping Plovers. Data are shown as mean \pm SD. Frequency variable is reported in Hz and temporal variable in msec.

Individuals	Number of calls	Dominant frequency of call	Duration of call	Interval between calls
Bp1m	8	2567 \pm 48	62 \pm 3	358 \pm 53
Bp2f	78	2869 \pm 98	62 \pm 5	403 \pm 77
Bp2m	34	2698 \pm 75	65 \pm 5	566 \pm 105
Cb3m	28	2533 \pm 50	48 \pm 5	359 \pm 86
Ch1f	58	2562 \pm 45	60 \pm 5	323 \pm 86
Ch1m	102	2556 \pm 68	75 \pm 15	414 \pm 134
Ch2m	105	2554 \pm 30	70 \pm 4	314 \pm 119
Ch4f	51	2545 \pm 67	62 \pm 7	405 \pm 137
Ch4m	57	2557 \pm 67	65 \pm 3	333 \pm 106
Cs11f	5	2733 \pm 49	59 \pm 3	356 \pm 78
Cs11m	49	2607 \pm 67	62 \pm 5	367 \pm 89
Cs1f	23	2631 \pm 60	83 \pm 5	359 \pm 86
Cs1m	50	2552 \pm 61	82 \pm 6	329 \pm 372
Cs2m	40	2635 \pm 82	60 \pm 7	323 \pm 82
Cs3f	9	2596 \pm 67	68 \pm 5	445 \pm 13
Cs4m	14	2596 \pm 76	67 \pm 3	294 \pm 20
Cs5f	51	2339 \pm 66	58 \pm 7	327 \pm 61
Cs5m	25	2401 \pm 58	63 \pm 8	312 \pm 13
Cs7f	8	2689 \pm 41	68 \pm 5	377 \pm 113

Appendix D. Continued.

Individuals	Number of calls	Dominant frequency of call	Duration of call	Interval between calls
Cs7m	21	2640 \pm 48	72 \pm 5	293 \pm 51
Cs8f	15	2667 \pm 57	58 \pm 3	219 \pm 38
Cs9f	10	2447 \pm 119	65 \pm 7	389 \pm 115
Cs9m	45	2623 \pm 37	64 \pm 5	324 \pm 5
Darf	47	2582 \pm 49	57 \pm 6	378 \pm 57
Grm	33	2507 \pm 28	54 \pm 2	352 \pm 44
Nrf	10	2313 \pm 82	69 \pm 5	349 \pm 69
Nrm	43	2509 \pm 44	67 \pm 5	428 \pm 97
Rc1f	21	2565 \pm 40	54 \pm 4	399 \pm 45
Rc1m	50	2453 \pm 101	54 \pm 3	299 \pm 59
Rc2m	11	2430 \pm 73	53 \pm 6	237 \pm 72
Rc 3f	33	2689 \pm 46	69 \pm 7	517 \pm 8
Rc3m	28	2430 \pm 154	83 \pm 4	345 \pm 62
Rc4m	15	2553 \pm 46	75 \pm 6	188 \pm 48
Rsf	45	2638 \pm 72	75 \pm 4	328 \pm 77
Rsm	80	2510 \pm 43	66 \pm 5	341 \pm 104
Saf	69	2733 \pm 50	58 \pm 3	455 \pm 106
Spf	19	2535 \pm 45	63 \pm 5	383 \pm 44
Total	1376	2577 \pm 129	65 \pm 10	363 \pm 132

