

The Condor 109:468–475
 © The Cooper Ornithological Society 2007

VARIATION AND INDIVIDUALITY IN DISPLAY-FLIGHT CALLS OF MALE PIPING PLOVERS

HA-CHEOL SUNG AND EDWARD H. MILLER¹

Biology Department, Memorial University, St. John's, NL, A1B 3X9, Canada

Abstract. In this first study of vocal individuality in the Charadriidae, we describe vocal variation in the endangered Piping Plover (*Charadrius melodus*). We studied a long-distance advertisement call given by breeding males during aerial displays, because functionally similar vocalizations of scolopacids are known to be individualistic. We analyzed recordings of 10 breeding males on Prince Edward Island, Canada, made in 1998 and 1999. Calls varied substantially among males: variance among males (in one-way ANOVAs) averaged 61% of the total variance across variables, similar to two scolopacid species. Males were distinguishable from one another even on the basis of single calls. However, discrimination ability (classification success) improved substantially when multiple-call averages per male were used; this approach more realistically represents how plovers experience one another's calls. Calls of two males changed little over days to weeks. In future work, individual identification can be improved by using averages from multiple calls. To improve techniques for application to the Piping Plover, we recommend research on marked individuals of common related species, which share many acoustic homologies.

Key words: *acoustic variation, individuality, Piping Plover, vocalization.*

Variación e Individualidad en las Llamadas de los Despliegues Aéreos de los Machos de *Charadrius melodus*

Resumen. En este primer estudio sobre individualidad vocal en la familia Charadriidae describi-

mos la variación vocal en el playero *Charadrius melodus*, una especie en peligro de extinción. Estudiamos una llamada de advertencia de larga distancia que es emitida por machos reproductivos durante sus despliegues aéreos, debido a que se conoce que llamadas funcionalmente similares presentan individualidad en los escolopácidos. Analizamos grabaciones de 10 machos reproductivos hechas en 1998 y 1999 en la isla Prince Edward, Canadá. Las llamadas variaron considerablemente entre machos: la varianza entre los machos (en un ANDEVA de una vía) correspondió en promedio al 61% del total de la varianza en todas las variables, de modo similar a lo observado en dos especies de escolopácidos. Los machos fueron distinguibles entre sí incluso con base en una sola llamada. Sin embargo, la habilidad de discriminación (éxito de clasificación) mejoró substancialmente cuando se utilizaron promedios de varias llamadas de un macho; este método representó de manera más realista el modo en que los playeros perciben las llamadas entre individuos. Las llamadas de dos machos cambiaron muy poco entre días o semanas. En trabajos futuros, la identificación individual puede ser mejorada con el uso de los promedios de múltiples llamadas. Para mejorar las técnicas y aplicarlas en *C. melodus*, recomendamos investigar individuos marcados de especies comunes relacionadas que compartan muchas homologías acústicas.

Social recognition serves diverse functions (Colgan 1983). Vocal recognition is particularly important in birds, serving to manage interactions involving pair members, group members, kin, or neighbors (Payne et al. 1991, Gonzáles and Ornelas 2005, Sharp and Hatchwell 2005). For example, distant vocal recognition between neighbors can obviate costly short-range interactions (Falls 1982, Stoddard 1996), and

Manuscript received 25 April 2006; accepted 16 January 2007.

¹ Corresponding author. E-mail: tmiller@mun.ca

individual recognition allows young chicks to reunite with parents or avoid attacks from unrelated adults in colonial species (Proffitt and McLean 1991, Searby et al. 2004). Individually distinctive vocalizations also have many applications in management or conservation, for example to estimate size or density of local populations, or to determine territory occupancy across years (Terry et al. 2005). Long-distance sound signals are particularly useful for the study of endangered species because sounds can be sampled with little or no disturbance to calling birds, including nocturnal and shy species (Peake et al. 1998, Rebbeck et al. 2001).

Two criteria must be met for vocalizations to be usable for individual recognition or in applied studies: within-individual acoustic variation should be low relative to among-individual variation; and vocal traits should be stable over time (Falls 1982, Charrier et al. 2004, Puglisi and Adamo 2004). These criteria are met for many different kinds of vocalizations (Dallmann and Geissmann 2001, Semple 2001, Volodin 2005). However, individuality may be most pronounced in long-distance vocalizations, because little information is available other than the signal itself to identify the caller, and because long-distance calls are often stereotyped as an adaptation for successful transmission (Schleidt 1973, Darden et al. 2003, Bosch and de la Riva 2004, Slabbekoorn 2004). In contrast, short-range calls can be more structurally variable, and information about an individual from short-distance calls is extensively augmented by information from optical cues, and environmental or social context (Smith 1977, 1997, Charrier, Jouventin et al. 2001). Individuality also may be particularly pronounced for innate vocalizations, because learned vocalizations can vary diurnally, seasonally, with age, with social context, and a variety of other factors (Kroodma 2004, Marler 2004, Chelen et al. 2005, Walcott et al. 2006). Finally, vocal individuality may be especially important in long-lived species that form long-term social bonds, or that re-encounter one another over successive years on breeding or wintering grounds. In summary, long-lived species with long-distance vocalizations that are not learned seem to offer high potential for studies of vocal recognition, and for applications in population monitoring. These characteristics apply to many species of shorebirds.

Shorebirds have diverse vocalizations, including long-distance nuptial calls that vary little within species, even over great geographic distances (Miller 1984, 1992, 1996). This vocal individuality in shorebirds may be particularly important for managing social interactions, and may be useful for applications to species of conservation concern, including long-lived resident species or migratory species with breeding-site fidelity across years (del Hoyo et al. 1996). Our present knowledge of shorebird vocalizations is based mainly on scolopacids (Miller 1992, 1995), in which vocal individuality has been documented for a few species (Howe 1972, Baker 1982, Miller 1982, 1986). Vocalizations are more poorly known for other shorebird taxa, for example Charadriidae, although individuality is suggested by

some accounts (Phillips 1977, Connors et al. 1993, Grønstøl 1996).

We quantified variation and individuality in a display call of the Piping Plover (*Charadrius melodus*). This species has a display repertoire and breeding system that appear to be typical of migratory Northern Hemisphere *Charadrius* species (Haig and Elliott-Smith 2004, Sung et al. 2005). The vocal repertoire is large and includes several long-distance display classes; furthermore, vocalizations are similar among individuals within populations, and also between populations in Atlantic Canada and Saskatchewan (Sung et al. 2005). Understanding the nature of vocal individuality in this species will improve our knowledge of its social biology, and will serve as a reference point for studies of many other species. Moreover, this species is of conservation concern, so knowledge of vocal individuality may contribute to techniques for population monitoring. Due to the difficulty of working with threatened and endangered species, refinement of analytical and experimental techniques may need to be done with common related species. Thus, using spectrograms, we compared vocal individuality of Piping Plovers and two abundant Charadriidae to support the validity of this approach.

METHODS

STUDY AREA, FIELD RECORDINGS, AND ACOUSTIC ANALYSIS

Male Piping Plovers (especially unpaired males) frequently engage in conspicuous aerial displays ("butterfly flights") that incorporate several kinds of loud vocalizations, including one that is repeated rhythmically in long series (Haig and Elliott-Smith 2004, Sung et al. 2005). We selected this call type (type A1a of Sung et al. 2005; Fig. 1A, 1B) for reasons given above, and because functionally similar call types in scolopacids are known to be individualistic (Miller 1982, 1986).

We studied plovers in Prince Edward Island National Park (46°25'N, 63°13'W), 1 May–30 July 1998 and 17 May–15 July 1999. Quantitative analyses reported below are based on samples selected from ~40 males: nine males recorded in 1998 (single samples for eight males; two samples separated by 14 days for one male); and one male recorded in 1999 (two samples separated by four days). It was not possible to record all males on the same date, because they were at different stages of the breeding cycle and large distances separated most of the birds. To ensure that we did not unintentionally record any males twice, we selected recordings of birds whose territories were well separated (up to 65 km) from one another. We used location of the territory in conjunction with repeated observations of individually idiosyncratic behavior (e.g., distinctive retreat or approach behavior in response to our presence) and individually distinctive external features (e.g., facial and breast markings) to confirm individual identity (Wilcox 1959, Parr 1980, Cairns 1982, Edwards 1982, Byrkjedal et al. 1997). To test for vocal stability over time, we recorded two distinctively marked birds in

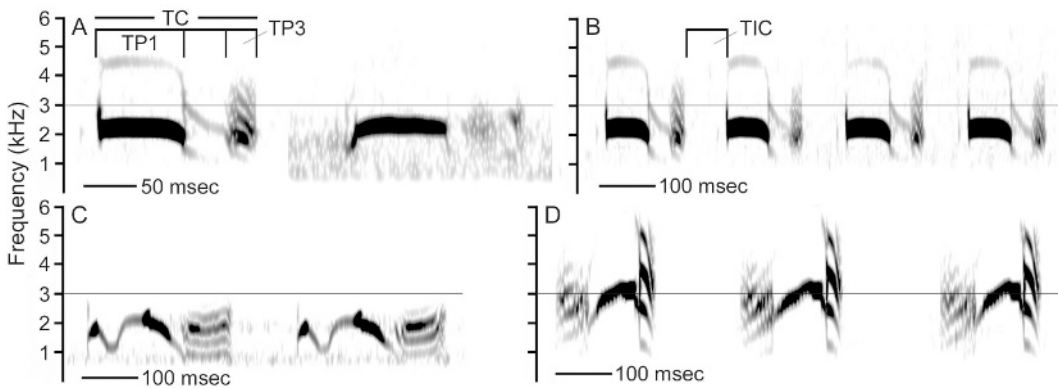


FIGURE 1. Butterfly-display calls of male Piping Plovers recorded in Saskatchewan and on Prince Edward Island, Canada, and of related species. (A) Single calls from Saskatchewan (left) and Prince Edward Island. Note the soft brief introductory element that is visible in the former but not the latter, in which it is masked by ambient noise. (B) Portion of long call sequence from Saskatchewan. (C) and (D) Portions of long call sequences from butterfly displays of Common Ringed Plover (two calls) and Semipalmated Plover (three calls), respectively. Saskatchewan Piping Plover recorded by EHM at Lake Diefenbaker, Saskatchewan, June 2004; Common Ringed Plover recorded by EHM near Longyearbyen, Svalbard, Norway, May 1994; Semipalmated Plover recorded by EHM on Middleton Island, Alaska, May 2003. TC is the total call duration; TIC is the interval between successive calls; TP1 and TP3 are the durations of the first and third call parts, respectively; and TWC (not shown; see text) is the interval between the first and third call parts.

isolated nesting territories on two different dates, as noted above.

We analyzed calls sampled from the middle of long call series (50+ calls), because they are loud, uttered rhythmically, and highly stereotyped (Miller 1983, Sung et al. 2005). Recordings were made with a Sony TC-D5PROII tape recorder and Telinga Pro-4 parabolic microphone with a flexible parabolic reflector (Telinga Microphones, Tobo, Sweden).

Call analyses were carried out on a personal computer with CSL 4300 and MultiSpeech software (Kay Elemetrics, Pine Brook, New Jersey). Calls were digitized at 25 kHz and analyzed with settings that established measurement precision as ± 1.68 msec for temporal and ± 16 Hz for frequency variables. The soft introductory notes apparent in Figures 1A and 1B could not be discerned on many spectrograms so were ignored in measurements (see the following descriptions). Temporal variables measured were: the interval between the beginning of the call and the beginning of the first call part (excluding the soft introductory element); the duration of the first call part (excluding the introductory element); the duration of the third (or final, in the case of compound calls) call part; the interval between the first and third call parts; and the interval between successive calls (this was measured from the end of the third part of a call to the beginning of the first part of the following call, so included the latter's introductory element; Fig. 1A, 1B). In addition, we measured the total call duration (again, ignoring the introductory element), but excluded this variable from certain analyses because it is redundant (= sum of the durations of the first call part, the interval between the first and third call parts, and the duration of the

third call part). Dominant frequency of the first and third call parts was measured to ± 16 Hz, using a power spectrum in bar mode. All spectrographic measurements were made on spectrograms prepared with ranges of 0–5 kHz and 2.5 sec, except for the interval from the beginning to the maximal frequency of the first call part; to improve measurement accuracy, that variable was measured on spectrograms prepared with a frequency range of 0–2 kHz.

STATISTICAL ANALYSES

Individuality can be expressed quantitatively in many ways, such as the coefficient of variation (CV). The added variance component among groups in analysis of variance (ANOVA) is a straightforward measure that is interpretable in terms of individuality (in this instance, variation among individual males [s^2_A] relative to total variance [$s^2 + s^2_A$]; Sokal and Rohlf 1981). This measure has the added advantage of being comparable across call types and species (Jenssen 1979, Miller 1982, Puglisi and Adamo 2004). We estimated variance components with one-way ANOVAs for each variable.

We also applied discriminant function analysis, which is widely used in studies of vocal individuality (Parsons and Jones 2000, Rebbeck et al. 2001). We used this technique with the raw data for the nine males from 1998. In addition, to determine whether discrimination ability could be improved by using multiple averages of a few calls each, we used (per male, with use of a random numbers table): 10 randomly chosen calls; five randomly chosen calls; five means, each based on two randomly chosen calls; 10 means, each based on two randomly chosen calls;

TABLE 1. Descriptive statistics and estimated added variance components (AVC) for butterfly-display calls of nine breeding male Piping Plovers recorded on Prince Edward Island, Canada, in 1998, using 20 calls per male.

Variable ^a	Grand mean \pm SD (range; CV _A ^b)	CV _W ^b	AVC ^c
FP1 (Hz)	2157 \pm 129 (1928–2339; 6)	3	84
FP3 (Hz)	2362 \pm 168 (1991–2524; 7)	5	62
TIC (msec)	67 \pm 22 (37–105; 32)	19	68
TIF (msec)	29 \pm 4 (20–36; 14)	14	47
TP1 (msec)	95 \pm 14 (76–116; 15)	7	77
TP3 (msec)	22 \pm 5 (20–24; 5)	10	21
TWC (msec)	48 \pm 11 (25–65; 23)	20	53
TC (msec)	165 \pm 15 (145–197; 9)	4	76

^a FP1 and FP3 are the dominant frequencies of the first and third call parts, respectively; TIC is the interval between successive calls; TIF is the interval between the beginning of the call and the beginning of the first call part; TP1 and TP3 are the durations of the first and third call parts, respectively; TWC is the interval between the first and third call parts; and TC is the total call duration.

^b CV (%): CV_A = among-male CV; CV_W = mean within-male CV (see Fig. 2).

^c Added variance component among males (s^2_A) as % of total variance (s^2) = $100s^2_A/(s^2 + s^2_A)$.

and five means, each based on four randomly chosen calls.

To investigate similarity across males in patterns of correlation among acoustic variables, we carried out principal components analysis (PCA; only data from the first recording date for the two males tested for seasonal variation were used) for multiple calls of each male, then measured concordance of the resulting variable scores on the first three PCs, using Kendall's coefficient of concordance, W (Sokal and Rohlf 1981). PCA also was carried out on male means, to complement the individual analyses. We used JMP[®] IN 5.1 (SAS Institute, Cary, North Carolina), SPSS 14.0 (SPSS, Inc., Chicago, Illinois), and S-plus 7.0 (Insightful Corp., Durham, North Carolina) for analyses.

To support our recommendation that pilot studies be conducted on related species, we compared spectrograms for Piping Plovers, Common Ringed Plovers (*Charadrius hiaticula*), and Semipalmated Plovers (*C. semipalmatus*) to illustrate homology among calls in features of organization and specific traits.

RESULTS

VOCAL VARIATION AND INDIVIDUALITY

Some general features of acoustic individuality were apparent (Fig. 1A, B); a quantitative summary is presented in Table 1. Each variable differed across males, with the added variance components averaging 61% (range: 21%–84%) of the total variance. Based on CVs, the dominant frequency of the first call part varied least (CV = 3%) among males, and the interval between successive calls and the interval between the first and third call parts varied most (CV ~20%; Table 1, Fig. 2).

Call samples were similar spectrographically across dates for the two males examined, but three variables differed slightly for the male sampled twice in 1999 (one-way ANOVAs): the dominant frequency of the first call part (2060 vs. 2085 Hz; $F_{1,62} = 10.2$, $P =$

0.002), the dominant frequency of the third call part (2203 vs. 2283 Hz; $F_{1,62} = 7.9$; $P = 0.007$), and the duration of the third call part (21.3 vs. 22.7 msec; $F_{1,62} = 8.0$; $P = 0.07$).

Discriminant function analysis using raw data for the nine males recorded in 1998 resulted in 5% misclassification of calls (Table 2). Classification improved substantially when analysis was based on variable means for two or four randomly chosen

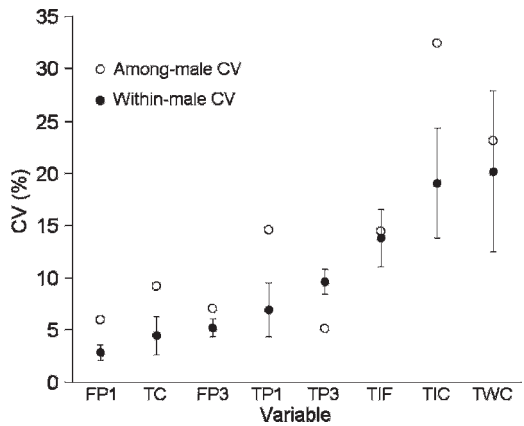


FIGURE 2. Variability profile (Yablokov 1974) for variables measured on butterfly-display calls of the Piping Plover, showing coefficients of variation (CV) of male means (values from Table 2), and mean \pm 1.96 SE for within-male CV ($r = 0.80$, all $P < 0.05$). FP1 and FP3 are the dominant frequencies of the first and third call parts, respectively; TC is the total call duration; TIC is the interval between successive calls; TIF is the interval between the beginning of the call and the beginning of the first call part; TP1 and TP3 are the durations of the first and third call parts, respectively; and TWC is the interval between the first and third call parts.

TABLE 2. Discriminant-function analyses of butterfly-display calls of nine breeding male Piping Plovers recorded on Prince Edward Island, Canada, in 1998: basic results and effects of data averaging. Eigenvalues, explained variance (%), and canonical correlation for the first three (of six) functions were: DF1, 6.2, 44%, and 0.93; DF2, 4.9, 35%, and 0.91; and DF3, 1.5, 11%, and 0.78.

Input data	Number of total (%) misclassified	Wilks's λ ($\times 10^6$)
Raw data		
All	15 of 290 (5)	1294
10 calls per male	7 of 90 (8)	868
5 calls per male	0 of 45 (0)	103
Means		
5 means, using 2 calls per male	0 of 45 (0)	8
10 means, using 2 calls per male	1 of 90 (1)	62
5 means, using 4 calls per male	0 of 45 (0)	1

calls, even with much lower sample sizes. For example, for five means based on four calls per male (for total $n = 20$ calls per male), misclassification was 0% and Wilks's $\lambda = \sim 10^{-6}$, several orders of magnitude less than solutions using raw data. The most important discriminating variables on the first two discriminant functions were duration of the first call part and dominant frequency of the first call part, respectively.

PATTERNS OF CORRELATIONS AMONG ACOUSTIC TRAITS

Acoustic traits within males were only loosely intercorrelated: mean $r = 0.66$ for the interval between call parts and the total call duration (all $P < 0.05$), but otherwise an $r > 0.5$ between traits occurred only twice in all the correlation matrices. The weak correlations between traits were reflected in individual PCAs: across males, explained variance was only 60%–70% for PC1–PC3 (each male had eigenvalues >1 for these PCs). Furthermore, patterns were similar across males: PC1, mean 28% (range: 23%–39%); PC2, mean 20% (range: 18%–23%); and PC3, mean 16% (range: 13%–19%). Despite the uniformity in explained variance across principal components, the particular acoustic traits contributing to the pattern differed across males: concordance (\bar{W}) across males for variable loadings on PC1–PC3 was not significant ($\chi^2_6 < 10.6$, $P > 0.1$ for all comparisons).

Little shared structure was apparent across males in terms of trait integration, although some association is suggested between the interval between successive calls and the duration of the first call part, and between the dominant frequency of the first call part and the dominant frequency of the third call part (Table 3).

The homologous butterfly-display calls of Common Ringed Plovers and Semipalmated Plovers are structurally similar to those of the Piping Plover in both general and specific features; for example, they are uttered rhythmically in long sequences, are brief, and include several call parts (Fig. 1C, D). Furthermore, even call parts are structurally similar (e.g., the brief, harmonically rich terminal call part).

DISCUSSION

VOCAL VARIATION AND INDIVIDUALITY

Acoustic traits differed in variability, with some being highly stereotyped (e.g., the dominant frequency of the first call part and the total call duration, CV $< 5\%$). However, most temporal measures were fairly variable, as occurs in many other species (Miller 1986, 1991). Therefore, levels and patterns of variation in acoustic traits in this species appear to be unremarkable.

Butterfly-display calls of Piping Plovers were stereotyped within and varied greatly among males, hence showed substantial individuality. Individual males could be readily distinguished from one another statistically, especially when they were

TABLE 3. Results of principal components analysis on male means of butterfly-display calls of 10 breeding male Piping Plovers recorded on Prince Edward Island, Canada, in 1998 and 1999. The explained variance (%) and eigenvalue are given in parentheses for each PC.

Variable ^a	Variable loadings		
	PC1 (41%, 2.9)	PC2 (27%, 1.9)	PC3 (15%, 1.1)
FP1	0.16	0.53	0.20
FP3	-0.37	0.51	0.06
TIC	0.51	0.14	-0.26
TIF	0.13	-0.48	0.60
TP1	0.49	-0.02	0.36
TP3	0.37	0.43	0.30
TWC	-0.43	0.12	0.56

^a FP1 and FP3 are the dominant frequencies of the first and third call parts, respectively; TIC is the interval between successive calls; TIF is the interval between the beginning of the call and the beginning of the first call part; TP1 and TP3 are the durations of the first and third call parts, respectively; and TWC is the interval between the first and third call parts.

characterized by multiple means based on several calls per mean. Quantitatively, variation among males (the mean of the added variance components = 63%, range = 21%–82%) was very similar to levels reported for functionally similar calls of males of the Least Sandpiper (*Calidris minutilla*; mean = 74%, range = 60%–82%; Miller 1986) and American Woodcock (*Philohela minor*; mean = 78%, range = 65%–90%; Miller 1982). Our lowest estimate was for a variable that was based on the soft terminal portion of these calls, and may have been low due to high within-male sample variation caused by recording conditions such as variability in recording distance or in orientation of the calling bird relative to the recording equipment. Estimates of the added variance component are lower in calls of some other nonpasserines: mean = 58% (range = 30%–68%) in Black-legged Kittiwakes (*Rissa tridactyla*; Miller 1982) and mean = 43% (range = 10%–74%) in Great Bitterns (*Botaurus stellaris*; Puglisi and Adamo 2004). The quantitative similarity of vocal individuality in Piping Plovers and scolopacids may reflect the functional similarity of the long-distance nuptial calls that have been studied; this interpretation could be tested by analysis of functionally different calls and of calls used for signaling over short distances.

Vocalizations of two males sampled on different dates showed little or no change over time. The small size of this sample, and the finding of a few significant differences between the samples for one male, indicate that further investigation is required. Effects of season or stage of the breeding season may have influenced our results, and should be addressed in future work.

In our analyses, even single calls of male Piping Plovers were attributed to different individuals with high accuracy. It is rarely the case that conspecific birds or scientists need to identify an individual based on a single call, however, so the use of discriminant function analysis or other quantitative techniques based on single calls seems both biologically inappropriate and unnecessary (Peake et al. 1998). Indeed, in some species repetition of calls is necessary for individual identification (Charrier, Mathevon et al. 2001). Several multiple-call averages per male are easy to obtain for Piping Plovers and many other shorebird species because they call frequently and often repetitively.

COVARIANCE STRUCTURE

Signal components vary in how they are correlated within individuals, but some correlation structure is universal, and substantial correlations among traits (particularly frequency traits) have been documented for many species (Hafner and Hafner 1979, Miller 1986). We noted a few significant positive correlations among acoustic traits of male Piping Plovers in this study (e.g., between the dominant frequency of the first call part and the dominant frequency of the third call part). Overall, however, correlations were only weak to moderate; furthermore, the pattern of trait correlations differed among males. The pattern of loose integration among traits suggests that the acoustic basis for individuality in this species is flexible, and is based on both specific traits that differ

among males and variable patterns of trait covariation.

Many acoustic homologies in vocal classes and traits occur between the Piping Plover and related species (this study, Miller 1996, Sung et al. 2005). These homologies offer opportunities for developing protocols for application to the endangered Piping Plover. Because of restrictions on studying endangered species, we recommend that a study of banded individuals of a related species be undertaken to refine sampling, measurement, and selection of variables and sample sizes; test identification protocols across breeding seasons; employ playback experimentation; and assess utility of multiple call types instead of single call types for individual identification (Fischer et al. 2001).

We thank staff and volunteers of Prince Edward Island National Park and Environment Canada (Canadian Wildlife Service) for encouragement and invaluable advice and help: D. Amirault, P. Ayles, E. Clow, S. Flemming, S. Gagnon-Provencher, P. Goossen, K. Kinneer, L. LaFosse, B. LeFresne, P. McCabe, P. McIntyre, J.-E. Proud, L. Thomas, and S. Westworth. I. Charrier and an anonymous reviewer provided many helpful comments on manuscript drafts. Funding was provided by the Canadian Wildlife Service, Memorial University, the Natural Sciences and Engineering Research Council of Canada (Discovery Grant to EHM), and Prince Edward Island National Park.

LITERATURE CITED

- BAKER, M. C. 1982. Individuality of vocalization in Dunlin: a possible acoustic basis for recognition of parent by offspring. *Auk* 99:771–774.
- BOSCH, J., AND I. DE LA RIVA. 2004. Are frog calls modulated by the environment? An analysis with anuran species from Bolivia. *Canadian Journal of Zoology* 82:880–888.
- BYRKJEDAL, I., G. B. GRØNSTØL, T. LISLEVAND, K. M. PEDERSEN, H. SANDVIK, AND S. STALHEIM. 1997. Mating systems and territory in Lapwings *Vanellus vanellus*. *Ibis* 139:129–137.
- CAIRNS, W. E. 1982. Biology and behavior of breeding Piping Plovers. *Wilson Bulletin* 94: 531–545.
- CHARRIER, I., L. L. BLOOMFIELD, AND C. B. STURDY. 2004. Note types and coding in parid vocalizations. I: The chick-a-dee call of the Black-capped Chickadee (*Poecile atricapillus*). *Canadian Journal of Zoology* 82:769–779.
- CHARRIER, I., P. JOUVENTIN, N. MATHEVON, AND T. AUBIN. 2001. Individual identity coding depends on call type in the South Polar Skua *Catharacta maccormacki*. *Polar Biology* 24:378–382.
- CHARRIER, I., N. MATHEVON, P. JOUVENTIN, AND T. AUBIN. 2001. Acoustic communication in a Black-headed Gull colony: how do chicks identify their parents? *Ethology* 107:961–974.
- CHELEN, A. A. R., C. M. GARCIA, AND K. RIEBEL. 2005. Variation in the song of a sub-oscine, the Vermilion Flycatcher. *Behaviour* 142:1115–1132.

- COLGAN, P. W. 1983. Comparative social recognition. Wiley, New York.
- CONNORS, P. G., B. J. MCCAFFERY, AND J. L. MARON. 1993. Speciation in golden-plovers, *Pluvialis dominica* and *P. fulva*: evidence from the breeding grounds. *Auk* 110:9–20.
- DALLMANN, R., AND T. GEISSMANN. 2001. Individuality in the female songs of wild silvery gibbons (*Hylobates moloch*) on Java, Indonesia. *Contributions to Zoology* 70:41–50.
- DARDEN, S. F., T. DABELSTEEN, AND S. B. PEDERSEN. 2003. A potential tool for swift fox (*Vulpes velox*) conservation: individuality of long-range barking sequences. *Journal of Mammalogy* 84:1417–1427.
- DEL HOYO, J., A. ELLIOTT, AND J. SARGATAL [EDS.]. 1996. Handbook of the birds of the world. Vol. 3: Hoatzin to auks. Lynx Edicions, Barcelona, Spain.
- EDWARDS, P. J. 1982. Plumage variation, territoriality and breeding displays of the Golden Plover *Pluvialis apricaria* in southwest Scotland. *Ibis* 124:88–95.
- FALLS, J. B. 1982. Individual recognition by sound in birds, p. 237–278. *In* D. E. Kroodsma and E. H. Miller [EDS.], *Acoustic communication in birds*. Vol. 2: song learning and its consequences. Academic Press, New York.
- FISCHER, J., K. HAMMERSCHMIDT, D. L. CHENEY, AND R. M. SEYFARTH. 2001. Acoustic features of female Chacma baboon barks. *Ethology* 107:33–54.
- GONZÁLES, C., AND J. F. ORNELAS. 2005. Song structure and microgeographic song variation in Wedge-tailed Sabrewings (*Campylopterus curvipennis*). *Auk* 122:593–607.
- GRØNSTØL, G. B. 1996. Aerobic components in the song-flight display of male Lapwings *Vanellus vanellus* as cues in female choice. *Ardea* 84:45–55.
- HAFNER, M. S., AND D. J. HAFNER. 1979. Vocalizations of grasshopper mice (genus *Onychomys*). *Journal of Mammalogy* 60:85–94.
- HAIG, S. M., AND E. ELLIOTT-SMITH [ONLINE]. 2004. Piping Plover. *In* A. Poole [ED.], *The birds of North America online*. Cornell Laboratory of Ornithology, Ithaca, NY. <http://bna.birds.cornell.edu/BNA/account/Piping_Plover/> (26 March 2006).
- HOWE, M. A. 1972. Pair bond formation and maintenance in Wilson's Phalarope, *Phalaropus tricolor*. Ph.D. thesis, University of Minnesota, Minneapolis, MN.
- JENSSEN, T. A. 1979. Display behaviour of *Anolis opalinus* (Sauria, Iguanidae): a case of weak display stereotypy. *Animal Behaviour* 27:173–184.
- KROODSMA, D. E. 2004. The diversity and plasticity of birdsong, p. 108–131. *In* P. Marler and H. Slabbekoorn [EDS.], *Nature's music: the science of birdsong*. Elsevier, Amsterdam.
- MARLER, P. 2004. Bird calls: a cornucopia for communication, p. 132–177. *In* P. Marler and H. Slabbekoorn [EDS.], *Nature's music: the science of birdsong*. Elsevier, Amsterdam.
- MILLER, E. H. 1982. Character and variance shift in acoustic signals of birds, p. 247–295. *In* D. E. Kroodsma and E. H. Miller [EDS.], *Acoustic communication in birds*. Vol. 1: production, perception, and design features of sounds. Academic Press, New York.
- MILLER, E. H. 1983. Structure of display flights in the Least Sandpiper. *Condor* 85:220–242.
- MILLER, E. H. 1984. Communication in breeding shorebirds, p. 169–241. *In* J. Burger and B. L. Olla [EDS.], *Shorebirds: breeding behavior and populations*. Plenum Press, New York.
- MILLER, E. H. 1986. Components of variation in nuptial calls of the Least Sandpiper (*Calidris minutilla*; Aves, Scolopacidae). *Systematic Biology* 35:400–413.
- MILLER, E. H. 1991. Communication in pinnipeds, with special reference to non-acoustic signaling, p. 128–235. *In* D. Renouf [ED.], *The behaviour of pinnipeds*. Chapman and Hall, London.
- MILLER, E. H. 1992. Acoustic signals of shorebirds: a survey and review of published information. Technical Report, Royal British Columbia Museum, Victoria, British Columbia, Canada.
- MILLER, E. H. 1995. Sounds of shorebirds: opportunities for amateurs and an update of published information. *Wader Study Group Bulletin* 78: 18–22.
- MILLER, E. H. 1996. Acoustic differentiation and speciation in shorebirds, p. 241–257. *In* D. E. Kroodsma and E. H. Miller [EDS.], *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, NY.
- PARR, R. 1980. Population study of Golden Plover *Pluvialis apricaria*, using marked birds. *Ornis Scandinavica* 11:179–189.
- PARSONS, S., AND G. JONES. 2000. Acoustic identification of twelve species of echolocating bat by discriminant function analysis and artificial neural networks. *Journal of Experimental Biology* 203:2641–2656.
- PAYNE, R. B., L. L. PAYNE, I. ROWLEY, AND E. M. RUSSELL. 1991. Social recognition and response to song in cooperative Red-winged Fairy-wrens. *Auk* 108:811–819.
- PEAKE, T. M., P. K. MCGREGOR, K. W. SMITH, G. TYLER, G. GILBERT, AND R. E. GREEN. 1998. Individuality in Corncrake *Crex crex* vocalizations. *Ibis* 140:120–127.
- PHILLIPS, R. E. 1977. Notes on the behaviour of the New Zealand Shore Plover. *Emu* 77:23–27.
- PROFFITT, F. M., AND I. G. MCLEAN. 1991. Recognition of parents' calls by chicks of the Snares Crested Penguin. *Bird Behaviour* 9:103–113.
- PUGLISI, L., AND C. ADAMO. 2004. Discrimination of individual voices in male Great Bitterns (*Botaurus stellaris*) in Italy. *Auk* 121:541–547.
- REBBECK, M., R. CORRICK, B. EAGLESTONE, AND C. STAINTON. 2001. Recognition of individual European Nightjars *Caprimulgus europaeus* from their song. *Ibis* 143:468–475.
- SCHLEIDT, W. M. 1973. Tonic communication: continual effects of discrete signs in animal

- communication systems. *Journal of Theoretical Biology* 42:359–386.
- SEARBY, A., P. JOUVENTIN, AND T. AUBIN. 2004. Acoustic recognition in Macaroni Penguins: an original signature system. *Animal Behaviour* 67: 615–625.
- SEMPLE, S. 2001. Individuality and male discrimination of female copulation calls in the yellow baboon. *Animal Behaviour* 61:1023–1028.
- SHARP, S. P., AND B. J. HATCHWELL. 2005. Individuality in the contact calls of cooperatively breeding Long-tailed Tits (*Aegithalos caudatus*). *Behaviour* 142:1559–1575.
- SLABBEKOORN, H. 2004. Singing in the wild: the ecology of birdsong, p. 178–205. *In* P. Marler and H. Slabbekoorn [EDS.], *Nature's music: the science of birdsong*. Elsevier, Amsterdam.
- SMITH, W. J. 1977. *The behavior of communicating: an ethological approach*. Harvard University Press, Cambridge, MA.
- SMITH, W. J. 1997. The behavior of communicating, after twenty years, p. 7–53. *In* D. H. Owings, M. D. Beecher, and N. S. Thompson [EDS.], *Perspectives in ethology*. Vol. 12: communication. Plenum Press, New York.
- SOKAL, R. R., AND F. J. ROHLF. 1981. *Biometry: the principles and practice of statistics in biological research*. 2nd ed. Freeman, San Francisco.
- STODDARD, P. K. 1996. Vocal recognition of neighbors by territorial passerines, p. 356–374. *In* D. E. Kroodsma and E. H. Miller [EDS.], *Ecology and evolution of acoustic communication in birds*. Cornell University Press, Ithaca, NY.
- SUNG, H.-C., E. H. MILLER, AND S. P. FLEMMING. 2005. Breeding vocalizations of the Piping Plover (*Charadrius melodus*): structure, diversity, and repertoire organization. *Canadian Journal of Zoology* 83:579–595.
- TERRY, A. M. R., T. M. PEAKE, AND P. K. MCGREGOR [ONLINE]. 2005. The role of vocal individuality in conservation. *Frontiers in Zoology* 2005, 2:10. <<http://www.frontiersinzoology.com/content/2/1/10>> (26 March 2006).
- VOLODIN, I. A. 2005. Individuality of alarm calls in the spotted suslik (*Spermophilus (Spermophilus) suslicus*, Rodentia, Sciuridae) [in Russian]. *Zoologicheskii Zhurnal* 84:228–235.
- WALCOTT, C., J. N. MAGER, AND W. PIPER. 2006. Changing territories, changing tunes: male loons, *Gavia immer*, change their vocalizations when they change territories. *Animal Behaviour* 71:673–683.
- WILCOX, L. 1959. A twenty year banding study of the Piping Plover. *Auk* 76:129–152.
- YABLOKOV, A. V. 1974. *Variability of mammals*. Amerind Publishing Company, New Delhi, India.