BRILL *Behaviour (2022)* DOI:10.1163/1568539X-bja10147 **Behaviour** brill.com/beh

# Anatomy of avian distress calls: structure, variation, and complexity in two species of shorebird (Aves: Charadrii)

**Edward H. Miller** [a,*,**], **Kristal N. Kostoglou** [b,***], **David R. Wilson** [c,****] and **Michael A. Weston** [b,*****]

[a] Biology Department, Memorial University, St. John's, NL, Canada A1C 5S7
[b] School of Life and Environmental Sciences, Deakin University, Burwood Campus, 221 Burwood Highway, Burwood, VIC 3125, Australia
[c] Psychology Department, Memorial University, St. John's, NL, Canada A1C 5S7
*Corresponding author's e-mail address: tmiller@mun.ca
**ORCID: https://orcid.org/0000-0003-2572-2272
***ORCID: https://orcid.org/0000-0003-0510-9059
****ORCID: https://orcid.org/0000-0002-6558-6415
*****ORCID: https://orcid.org/0000-0002-8717-0410

Received 2 September 2021; initial decision 8 November 2021; revised 16 December 2021; accepted 16 December 2021; published online 7 January 2022

---

## Abstract

Birds often vocalize when threatened or captured by a predator. We present detailed qualitative analyses of calls from 24 red-capped plover (*Charadrius ruficapillus*) and 117 masked lapwing (*Vanellus miles*) chicks (Charadriidae) that we recorded during handling. Calls were structurally complex and differed between species. Calls showed moderate structure at higher levels of organization (e.g., similarity between successive calls; sequential grading). Some call characteristics resembled those in other bird species in similar circumstances (e.g., in nonlinear phenomena). Most calls consisted of several different parts, which combined in different ways across calls. Past studies have overlooked most features of distress calls and calling in charadriids due to small sample sizes and limited spectrographic analyses. Understanding interspecific patterns in call structure, and determination of call functions, will require: detailed knowledge of natural history; detailed behavioural descriptions, acoustic analysis, and analyses of development and growth; and experimental investigations of call functions.

## Keywords

*Charadrius ruficapillus*, distress call, masked lapwing, red-capped plover, *Vanellus miles*, vocal development.

## 1. Introduction

Many animals utter distinctive calls when threatened or captured by a predator. Such so-called ‘distress calls’ are widespread and can be strikingly similar in structure across distantly related forms, including lizards, mammals, and birds (Davis, 1988, 1991; Marler, 2004; Amaya et al., 2019; Ruiz-Monachesi & Labra, 2020). Diverse proximate and ultimate functions of distress calls have been proposed. Calls may serve to startle the predator; attract other predators that compete with the first one and enable the caller to escape; or attract individuals of the same or different species that attack, mob, or distract the predator (Högstedt, 1983; Klump & Shalter, 1984; Davis, 1991; Marler, 2004; Zuberbühler, 2009; Carro & Fernández, 2021). These varied possibilities are paralleled by varied interpretations of how distress calls evolve, for example through natural selection acting directly on the vocalizing individual, altruistic selection, or kin selection (Rohwer et al., 1976; Davis, 1991). Testing these hypotheses will require knowledge about the natural history and behaviour of each species, determination of the identity of the intended receiver(s) and determination of the distance(s) over which distress calls are adapted for transmission (i.e., the active space — e.g., short distances for nearby siblings or longer distances to reach parents or other adult birds in the vicinity). Transmission distance is important for understanding structural adaptations in calls because sounds change over distance (e.g., in amplitude and frequency spectrum), hence acoustic displays differ in structure between those adapted for communication over short vs. long distances (Morton, 1977; Marler, 2004; Bradbury & Vehrencamp, 2011a; Wiley, 2015). It follows that information about the structure of distress calls is essential for testing adaptive or functional hypotheses and interpreting experimental results. Knowledge about structure also is needed above the level of individual calls, such as how calls are patterned over call sequences. For example, distress calls are repeated rapidly in many birds (Davis, 1988; Marler, 2004), presumably because the property of rapid repetition is adaptive. Other properties of call sequences (e.g., short-term variety, which may startle a predator) also may be adaptive, hence should be included in descriptions.

Many or all species of shorebird utter calls when captured (e.g., in mist nets) or handled, at all ages. Adult and immature birds give such calls throughout the year, though incidence and patterns vary across species. Shorebird biologists refer to these calls broadly as ‘distress calls’. The calls can attract the attention of and elicit close approach from birds of the same or different species, sometimes in substantial numbers, and so have been used widely to attract shorebirds for banding (Gratto-Trevor, 2018). The adaptive functions of such calls are unclear. We analyzed calls given by shorebird chicks when they were held in the hand for banding, taking measurements, and sampling blood. Focusing on calls given in this narrow circumstance may facilitate understanding of structure and function of distress calls more broadly.

We studied sound recordings of chicks made opportunistically during field research on the red-capped plover (*Charadrius ruficapillus*) and the southern subspecies of masked lapwing (*Vanellus miles novaehollandiae*; del Hoyo et al., 2020; Kostoglou et al., 2017, 2020, 2021; Lees et al., 2018, 2019; 'plovers' and 'lapwings' hereafter). Elsewhere, we analyze relationships of acoustic structure to sex and body size based on several quantitative traits (Kostoglou et al., 2022). Here we provide an in-depth qualitative analysis of calls. Knowledge of acoustic structure is crucial to many areas of investigation. The importance of baseline descriptions can be illustrated with a publication that is nearly 70 years old, on calls of the domestic fowl (*Gallus gallus*; Collias & Joos, 1953): that publication has been cited nearly 400 times in a broad range of basic and applied research areas, including in recent publications (e.g., Herborn et al., 2020).

We describe call features, organization, and variation within and between the study species, to provide the most detailed descriptions of chick calls to date for any species of Charadriidae. The descriptions can be used as a basis to investigate specific features of calls in relation to function, different treatments (e.g., in heat-stressed chicks), in developmental or comparative studies, and so on. They also provide a framework for other workers, who may be able to collect additional data from chicks they handle already for other purposes, by applying simple, opportunistic, and non-invasive sound recording procedures.

We based the following descriptions on the premise that detailed knowledge of call repertoires and structure is an essential starting point for future studies. The alternative would have been to make coarser (simpler) descriptions that may be more interpretable in our present state of knowledge, but would deny potentially useful information about call structure and variation to future investigators. We opted instead for descriptions that are as accurate and complete as possible to promote repeatability, interpretability, and scalability (Berman, 2018). In the same spirit, we avoided the use of many subjectively defined categories of calls, which has a similar consequence (Beer, 1977; James & McCulloch, 1985; Fischer et al., 2016). Instead we identified only several broad classes of call for each species; future studies will determine whether discrete structurally based classes occur in all or part of the species' repertoires. It was not possible to assess individual differences because we recorded most birds only once, so apparent differences between individuals may merely reflect differences between recording sessions.

We anticipated that our findings would support several established trends. First, distress calls would be brief, relatively simple in structure, and structurally variable, as in chicks of other precocial species (Collias & Joos, 1953; Marx et al., 2001; Adret, 2012; Dragonetti et al., 2013a, b). Nevertheless, nonlinear phenomena (resulting from desynchronization of sound-production mechanisms in the vocal tract) are apparent in some accounts (Dragonetti et al., 2013b), so we expected to observe them also. Second, we expected to find strong similarities between calls of the study species. This expectation was based on the observation that the structure and repertoires of acoustic displays in shorebirds have evolved slowly, even for nuptial displays that commonly evolve rapidly through social selection (Miller & Baker, 2009; Tobias et al., 2020). Therefore, we anticipated that call structure and repertoires would be similar between the study species, particularly for young chicks (Gottlieb & Vandenbergh, 1968; Klenova & Koleshnikova, 2013). Modern estimates suggest more recent divergence times than in past studies (e.g. Baker et al., 2007), but nevertheless the two clades that include our study species are quite old (the clades may have diverged from one another as recently as the Oligocene, approx. 30+ mya; Černý & Natale, 2021). We could not make detailed predictions about the nature of vocal divergence because very few spectrographic analyses of chick calls in *Charadrius* and *Vanellus* species are available. Our third expectation was that the species' calls would differ in frequency traits because the species differ so greatly in body size (adult masked lapwings weigh about ten times as much as red-capped plovers; see below), and frequency and body mass tend to be inversely related in birds (Ryan & Brenowitz, 1985; Francis & Wilkins, 2021). We address only the first two expectations in this paper; the third is analyzed in Kostoglou et al. (2022).

Below we describe call structure and variation for each species. First, we treat traits, trait variation, and trait organization at the level of the individual call. Then we describe aspects of organization above the level of the call, including intergradation across successive calls (a pattern variously referred to as drift, sequential or adjacent grading, etc.; Andrew, 1969; Marler, 1976; Green & Marler, 1979; Miller, 1979).

On its surface, the term ‘distress call’ is a poor label for a behavioural category: it is interpretive rather than descriptive, and implies functions that reflect an observer’s view; it includes a word (‘distress’) that in itself has no widely accepted definition; the category, its acoustic properties, and its control mechanisms surely are not homologous across species; mechanisms and functions of the calls obviously must vary greatly across age, sex, social class, stage of the annual cycle; and so on (Marler, 2004). Nevertheless, if such terms are described and defined clearly enough to be interpretable and independently repeatable in other studies, we feel that their use is defensible (Miller & Kochnev, 2021). Our labelling of calls of hand-held plover chicks as ‘distress calls’ falls in this category.

## 2. Material and methods

The following summary is based on Temple-Smith (1969), Moffat (1981), Marchant & Higgins (1993), del Hoyo et al. (2020), Mo (2020), Wiersma et al. (2020), and personal observations.

Red-capped plovers commonly nest on coastal sandy or shell beaches, and bare areas at inland wetlands or anthropogenic habitats (e.g., sewage ponds), etc. (details in Wiersma et al., 2020). In Australia, they breed over an extended period that encompasses the austral summer (December–February). They nest in open habitat or under low vegetation; clutch size is 1–2. The species is small (body mass 35–40 g) and sexually dichromatic (males have bright red heads, and females generally have duller orange heads) but the sexes are similar in body size. Parental care is shared more-or-less equally between the parents, though females tend to incubate by day and to rear female-dominated broods (Ekanayake et al., 2015; Lees et al., 2018). We studied plovers from October 2017 to March 2018 in Cheetham Wetlands, Point Cook, VIC, Australia (37°54′S, 144°47′E), where nests are protected by predator-exclusion cages (Tan et al., 2015).

Masked lapwings in Australia commonly inhabit both rural and urban habitats. They breed from June-October, usually in open habitat (e.g., sporting ovals or farmland); clutch size is normally 3–4. They are large (body mass 296–412 g) and sexually monochromatic; the sexes are similar in body size. We studied a lapwing population from June to September 2018 on Phillip Island, VIC, Australia (38°29′S, 145°14′E), where the species is abundant. For more details about study sites, see Kostoglou et al. (2017, 2020, 2021).

During the breeding seasons, and for both species, we searched for nests 4–5 days per week by walking or driving along numerous routes while using binoculars and spotting scopes to search for adults that were engaged in nest-building behaviour (e.g., scraping) or were incubating. We estimated the age of eggs by flotation (Liebezeit et al., 2007), assuming incubation periods (from the completion of laying) of 30–31 days for plovers and 32 days for lapwings. We usually visited nests only once after we found them, to minimize disturbance. We timed that visit to coincide with hatching, as determined by the estimated age of eggs. We took standard body measurements and blood samples for sex determination (Kostoglou et al., 2017, 2020, 2021; Lees et al., 2018, 2019), and recorded calls while doing so. We opportunistically captured some older chicks in families that we had not captured previously, and we processed them similarly. We did not know the age of many chicks, and age estimation based on linear body measurements was unreliable, so body mass was used as a proxy for age by Kostoglou et al. (2022); here (in the Appendix), we report body mass and some ages for chicks whose calls are analyzed spectrographically in this paper.

We processed all chicks in a quiet, sheltered location, usually the inside of a vehicle. It took about 15 min to process each chick. Most chicks called while we held them. We recorded vocalisations from chicks in the hand with a Roland R-26 portable digital recorder and omnidirectional Sennheiser ME 2-II microphone (frequency range, 50 Hz to 18 kHz) held approx. 5 cm from the chick. The recorder settings were 44.1 kHz sampling rate and no pre-emphasis. When broods contained more than one chick, we put chicks in separate bags and processed them separately.

We analyzed 3495 calls from 32 recordings of plover chicks (1–334 calls per recording; median 128). These represented 24 individuals because we recaptured and re-recorded five plover chicks several times. Plovers did not call in three recordings. We analyzed 6835 calls from 117 individual lapwing chicks (1–336 calls per chick; median 35); we recaptured no lapwing chicks. Lapwings did not call in 17 recordings.

We normalized recordings at 24-bit resolution with Audacity 3.0.2 (audacityteam.org). We inspected recordings with seewave 2.1.6 (rug.mnhn.fr/seewave), Praat (praat6142, 16-bit edition; https://www.fon.hum.uva.nl/praat/), or Raven Pro 1.6 (ravensoundsoftware.com/software/raven-pro/). We prepared illustrations in Inkscape 1.0.2 (inkscape.org) from waveforms and spectrograms produced in Raven Pro. We used the following analytical settings for spectrograms, except as indicated in some figure legends: Blackman window; 324 sample points (=7.35 ms); 89.8% overlap; and DFT size, 512 (=86.1 Hz). We used a few different time and frequency scales to accommodate variation across calls (e.g., calls of low vs. high frequency) and to serve purposes of different figures.

We used published and unpublished sources for comparison with our findings. We supplemented the few published analyses of *Charadrius* calls by analyzing chick calls of Wilson's plover (*Ch. wilsonia*) in the Macaulay Library (https://www.macaulaylibrary.org/; ML223948). We found no published analyses of chick calls in *Vanellus*, so analyzed sounds of red-wattled lapwing (*V. indicus*) and northern lapwing (*V. vanellus*) from YouTube videos wg6FBQLYeW4 and xK66jx43tNU, respectively. We also examined calls in a second YouTube video of a newly hatched chick red-wattled lapwing at its nest alone with three eggs (aYJqKWnhEic).

We use the term modulation below. This term has many general meanings, such as "a change in the style, loudness, etc. of something [like] voice" (Cambridge Dictionary, 2021). In acoustics, electrical engineering, telecommunications, and other fields, the word has more specific meanings in reference to modulation of amplitude (AM) or frequency (FM) of a sinusoidal signal (Bradbury & Vehrencamp, 2011b; Ginsberg, 2018). Most birds do not utter pure-tonal sinusoidal sounds, so it is not technically correct to refer to AM and FM in most cases ('periodic nonsinusoidal signal' is the term suggested by Bradbury & Vehrencamp, 2011a, b). Nevertheless, approximations to AM and FM occur in many bird sounds (Greenewalt, 1968; Stein, 1968; Marler, 1969), so we use the term to refer to "changes in amplitude or frequency (e.g., a call's dominant frequency) that are approximately rhythmic". We use the more general term 'periodicity' in reference to the approximately rhythmically repeated broadband sections of sound in the commonest kind of plover call (i.e., Class I Calls; see below).

## 3. Results

### *3.1. Red-capped plover*

FM was prominent in most calls but varied greatly in expression. For convenience in description, we considered calls with periodicity (AM or FM, even when the latter was obscured due to deterministic chaos [see further]) to be a single class (Class I Calls). These were the commonest kind of call

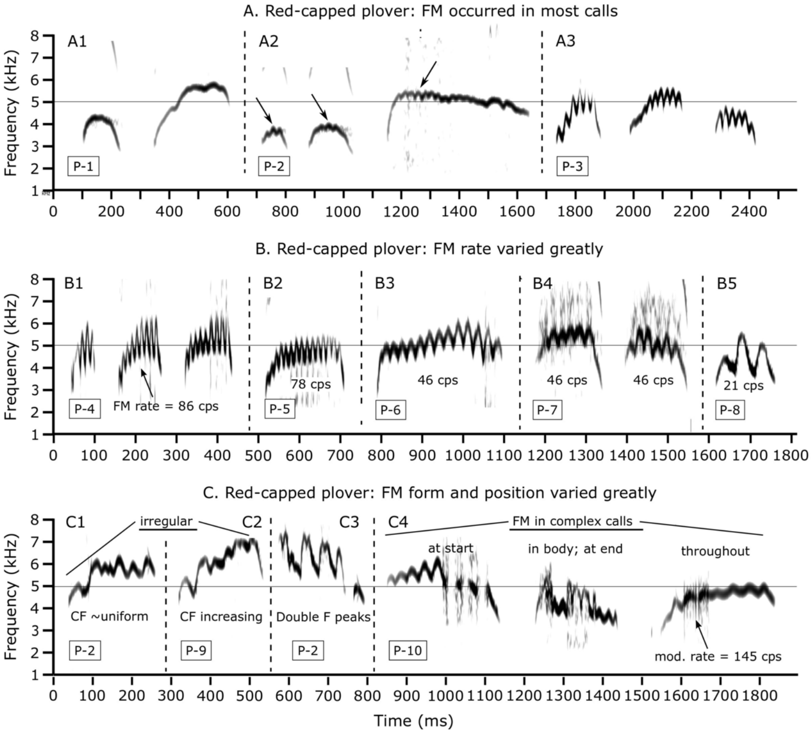


**Figure 1.** Frequency modulation (FM) in calls varied greatly within and across red-capped plover chicks. (A) Calls varied in the frequency range they covered; small fluctuations in frequency are marked by arrows in A2. (B) FM varied greatly in rate across calls. (C) FM sometimes was irregular or complex, and varied in presence or extent in complex calls; extremely rapid FM was rare. Calls in panels A1–A3, B1, B4, and C4 were not successive and the intervals shown between them are arbitrary. Plover chick numbers (P-) denote different individuals, and are consistent within and across figures. Information on body mass, sex, and age (when known) is in the Appendix. The horizontal lines at 5 kHz are visual guides. Analysis settings are as stated in Methods, except for panel A, for which number of points per analysis frame = 512. Abbreviations: cps, cycles per second; CF, carrier frequency; F, frequency.

in our sample. Periodicity was expressed most simply as FM (Figures 1–3). Usually calls with FM also had extensive broadband ‘noise’, resulting from the nonlinear phenomenon of deterministic chaos (hereafter DC; Wilden et al., 1998; Beckers & ten Cate, 2006; Digby et al., 2013).

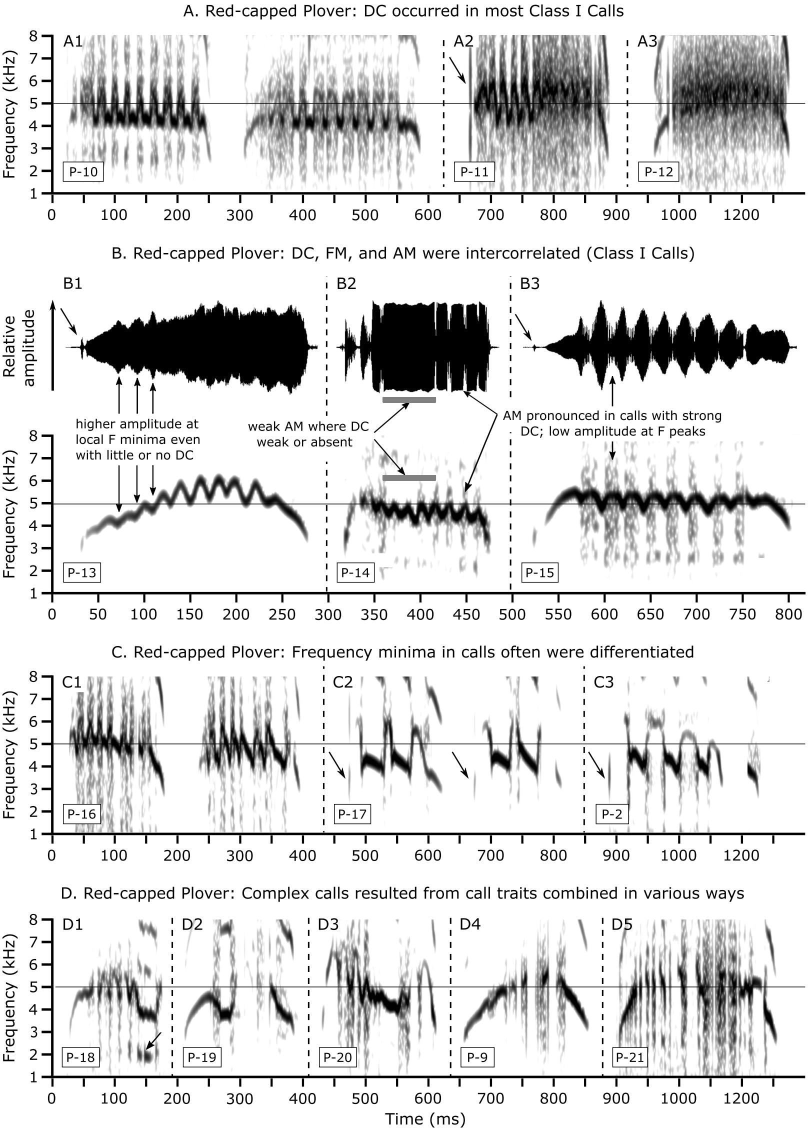
The frequency range of Class I Calls varied greatly because: (1) the general trajectory of frequency spanned different frequency ranges across calls (Figure 1A1–A3); and (2) the frequency range covered by FM fluctuations varied greatly: compare calls in Figure 1A2 (right), 1A3, and 1B.

The rate of modulation varied within and across calls. It often declined over a call (e.g., Figure 1B3), and varied about 4-fold across calls (about 21–86 cps) for calls in Figure 1B. Its temporal pattern sometimes was slightly irregular (Figure 1C1–C2) or complex (compound modulations in Figure 1C3). FM occurred throughout or at different places within calls (Figure 1C4). Calls with lengthened frequency maxima or minima of course had slower repetition rates (see further). Very rapid modulation was rare, and occurred as discrete sequences once or several times within calls (Figure 1C4 call on right). A single sharp pulse (sometimes several pulses) preceded most Class I Calls (Figure 2A2, 2B1, 2B3, 2C3).

DC was expressed most strongly at frequency peaks in calls with periodicity (e.g., Figure 2A1). Sometimes DC obscured frequency structure or periodicity partly or completely (Figure 2A2–A3). A striking feature of frequency and DC was their association with one another and with amplitude. Amplitude peaks in the waveform were associated weakly with minimal frequency in calls that lacked DC (Figure 2B1; first part of Figure 2B2). However, that relationship was pronounced when approx. rhythmic DC was present because DC was associated so strongly with low amplitude (Figure 2B2–B3). This imparted a vertically striated pattern on spectrograms to all or parts of calls with periodicity (Figure 2A1–2A2, 2B3, 2C1, etc.). The striations revealed the presence and enabled measurement of rates of periodicity even when frequency peaks were not visible.

The rate of FM in Class I Calls was fastest when inflection points at frequency minima and maxima were sharp and frequency changed quickly (i.e., had a steep slope) between those points (e.g., Figure 1B1–B2). Rate was slower if inflection points were not sharp or if frequency changed gradually between them (Figure 1B5, 1C4 call on right; Figure 2B1–B3).

Both DC and non-DC portions of periodicity varied in duration in Class I Calls. The low-frequency tonal segments (i.e., consisting of the fundamental



A. Red-capped Plover: DC occurred in most Class I Calls

B. Red-capped Plover: DC, FM, and AM were intercorrelated (Class I Calls)

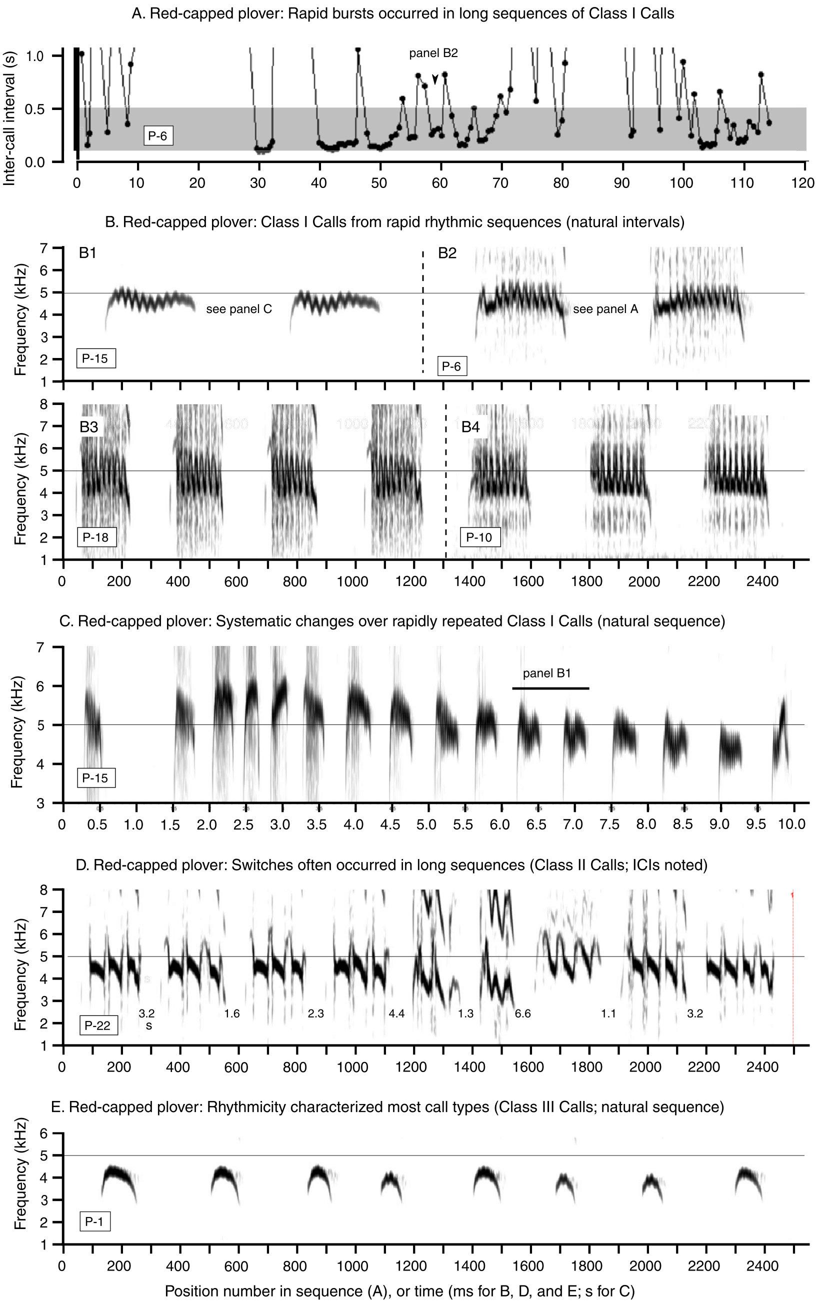
C. Red-capped Plover: Frequency minima in calls often were differentiated

D. Red-capped Plover: Complex calls resulted from call traits combined in various ways frequency and various harmonics) between successive rhythmically repeated DC segments of calls often lengthened, leading to increased temporal separation of DC segments (e.g., both calls in Figure 2A1). The degree of lengthening varied within and across calls (Figure 2C). Call doublets, triplets, etc., were suggested when frequency minima were lengthened substantially and separated by sharp (e.g., first call in Figure 2C2) or low-amplitude (e.g., second call in Figure 2C2) peaks. Despite the structural commonality between Class I Calls and such calls, we recognized the latter (e.g., Figure 2C2–C3, Figure 3D (first four and last two calls)) as a different call class (Class II).

The acoustic traits described above, in combination with temporal breaks, pulses, combinations of different patterns of periodicity, etc., produced highly varied calls (Figure 2D). Two nonlinear phenomena other than DC are common in bird vocalizations: subharmonics and frequency jumps (SH and FJ, respectively; Wilden et al., 1998). In plover calls, SHs occurred fairly often but usually were weak (Figure 2D1); we observed no FJs.

The temporal pattern of delivery of Class I Calls varied from approx. rhythmic repetition in short to long bursts (Figure 3A-C) to single calls uttered irregularly. We observed no kind of call that we could consider as a trill (e.g., as couplets, triplets, or longer series). The interval between rapidly repeated Class I Calls sometimes was very brief (approx. 110 ms in Figure 3A; <80 ms in some sequences: Kostoglou et al., 2022). On a small temporal scale, successive Class I Calls in bursts were similar to one another (Figure 3B), but gradual variation over sequences was common (e.g., in call duration, inter-call interval, and frequency; Figure 3C). The tendency to utter similar calls in sequence even characterized slowly repeated calls;

**Figure 2.** Class I Calls of red-capped plover chicks varied in the expression and placement of deterministic chaos (DC), the structure of non-DC tonal parts of calls, and frequency and amplitude modulation (FM, AM; A). (B) Amplitude and frequency in Class I Calls were negatively linked, a trend that was clearest mainly in calls with strong DC, which occurred at frequency maxima. (C) Frequency minima between frequency peaks varied from brief to long in Class I Calls (C1); they were characteristically long in Class II Calls (C2–C3). (D) Complex calls resulted from the presence of subharmonics (arrow in D1), or because different qualities changed in duration or were recombined. Pulses occurred before most calls (marked by arrows in A2, B1, B3, C2, and C3). Calls in A1, A2, C1, and C2 were not successive and the intervals shown between them are arbitrary. Plover chick numbers (P-) denote different individuals, and are consistent within and across figures. Information on body mass, sex, and age (when known) is in the Appendix. The horizontal lines at 5 kHz are visual guides. Analysis settings are as stated in Methods.


A. Red-capped plover: Rapid bursts occurred in long sequences of Class I Calls
Inter-call interval (s)
1.0
0.5
0.0
panel B2
P-6
0
10
20
30
40
50
60
70
80
90
100
110
120
B. Red-capped plover: Class I Calls from rapid rhythmic sequences (natural intervals)
Frequency (kHz)
B1
see panel C
P-15
B2
see panel A
P-6
B3
P-18
B4
P-10
0
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
2400
C. Red-capped plover: Systematic changes over rapidly repeated Class I Calls (natural sequence)
Frequency (kHz)
panel B1
P-15
0
0.5
1.0
1.5
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
6.0
6.5
7.0
7.5
8.0
8.5
9.0
9.5
10.0
D. Red-capped plover: Switches often occurred in long sequences (Class II Calls; ICIs noted)
Frequency (kHz)
3.2 s
1.6
2.3
4.4
1.3
6.6
1.1
3.2
P-22
E. Red-capped plover: Rhythmicity characterized most call types (Class III Calls; natural sequence)
Frequency (kHz)
P-1
0
200
400
600
800
1000
1200
1400
1600
1800
2000
2200
2400
Position number in sequence (A), or time (ms for B, D, and E; s for C)

an example for Class II Calls (with a switch to other sorts of calls within the sequence) is shown in Figure 3D. We observed a kind of brief tonal call only in one recording (Class III Calls; Figure 3E). It occurred singly or in rhythmic sequences. These calls were in the second of three sound recordings made at different ages for a single chick; Class I Calls dominated that chick's first and third recordings.

### *3.2. Masked lapwing*

Most lapwing calls were predominantly tonal. The simple structure of a common form included a brief rapid rise to a frequency maximum, followed by a gradual decline in frequency (Figure 4A1–A2, 4A6), ranging to a sharp drop followed by a gradual decline (Figure 4A). This simple form was commonly given by birds in the hand (Figure 4A1–A5) and also was the main form of call uttered by background chicks held in bags (Figure 4A6). These calls varied greatly and graded into simpler calls (Figure 4C). We considered them together as Class I Calls; as for plovers, we recognize that they may not constitute a natural structural class.

Class I Calls rarely were preceded by a pulse, and varied greatly at the start (Figure 4A–B). The initial frequency peak ranged over >4 kHz across calls, and varied from being sharply peaked (e.g., Figure 4A3–A5, 4B1, 4B3) to slightly or even extensively rounded (Figure 4A1–A2, 4A6, 4B2, 4B6). The introductory peak ranged from high (some to >8 kHz) to only slightly higher than the remainder of the call (Figure 4A1, 4A3, 4C1–C2); sometimes no peak occurred (Figure 4C3–C6). Most Class I Calls were

---

**Figure 3.** The temporal pattern of call delivery by red-capped plover chicks varied within and across call types. (A) Class I Calls were uttered irregularly but often were given in bursts, with brief intervals between calls. (B) Four examples of successive Class I Calls from bursts; natural intervals are shown. (C) Successive gradation in call characteristics occurred over bursts of Class I Calls, despite close similarity between immediately successive calls (spectrogram shown on limited frequency scale, to emphasize changes in frequency; natural intervals shown). (D) Class II Calls frequently were given irregularly in long sequences, though not commonly in bursts. In the sequence illustrated, three other kinds of call were given before Class II Calls resumed (intervals between successive calls noted). (E) The uncommon tonal Class III Calls sometimes were given in approx. rhythmic sequences (part of longer sequence shown; natural intervals between calls are shown). Plover chick numbers (P-) denote different individuals, and are consistent within and across figures. Information on body mass, sex, and age (when known) is in the Appendix. The horizontal lines at 5 kHz are visual guides. Frequency scales in panels B and E were cropped to economize on space. Analysis settings are as stated in Methods. ICI = Inter-Call Interval.

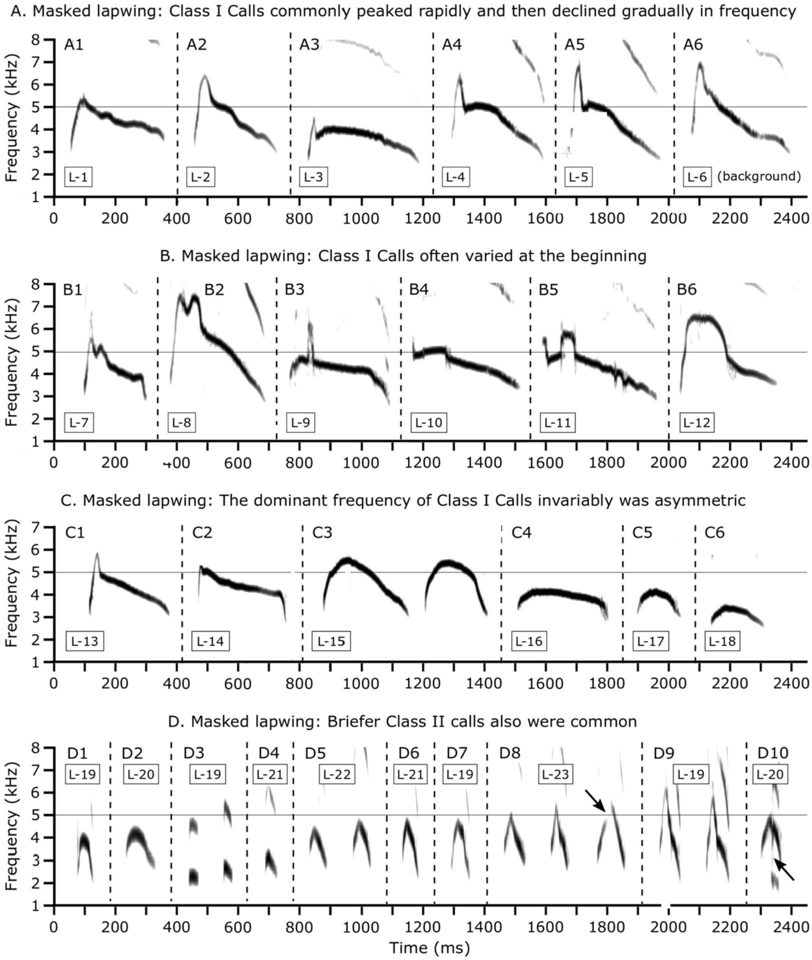


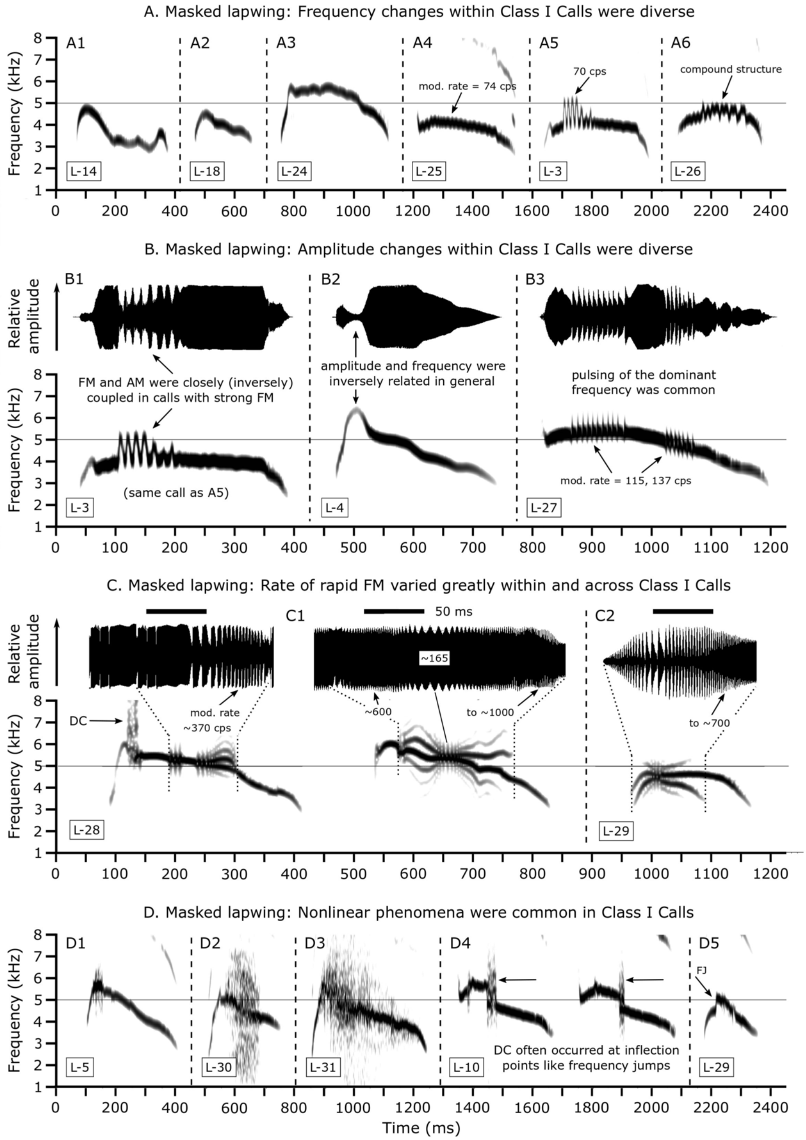
**Figure 4.** We recognized several broad classes of calls of masked lapwing chicks. (A) Class I Calls were long and tonal. They often began with a sharp rise in frequency, followed by a slower decline. (B) The start of Class I Calls was variable. (C) Class I Calls often began with little or no frequency rise, but the trajectory of dominant frequency was almost always asymmetric in frequency. (D) Class II Calls were brief vocalizations. The arrows point to a frequency gap due to low amplitude (D8) and deterministic chaos (D10). Calls in C3, D3, D5, D8, and D9 were not successive and the intervals shown between them are arbitrary. Lapwing chick numbers (L-) denote different individuals, and are consistent within and across figures. Information on body mass, sex, and age (when known) is in the Appendix. The horizontal lines at 5 kHz are visual guides. Analysis settings are as stated in Methods, except number of points per analysis frame = 512 for panels A–C, and 256 for panel D.

strongly asymmetric across their course because frequency rose quickly at or near the beginning of the call, then declined more slowly. Asymmetry to some degree was almost universal however: weak asymmetry can be seen in Figure 4C, and extremely weak asymmetry in Figure 4C4–C6. Class I Calls varied in other ways as well, in frequency range, duration, the trajectory of the dominant frequency, variations in the dominant frequency, etc. (Figure 4). We discuss these and other aspects of Class I Calls below.

Lapwings also uttered many brief calls, which differed in duration and emission pattern from Class I Calls (for example, some brief calls occurred regularly as sets; see below). We describe delivery patterns below; here we describe brief calls as individual entities.

We included some brief calls within Class I Calls (e.g., Figure 4C5–C6) but recognized others as a distinct class. Class II Calls were extremely brief (most $<$ 100 ms in duration) and were characterized by a rapid rise in frequency to a peak, followed by a slightly slower frequency decline to the end (Figure 4D). Frequency changes around the peak ranged from gradual (Figure 4D1–D2) to sudden (i.e., the peak was sharp; Figure 4D8–D9). Frequency around the peak was lowest in amplitude, as for Class I Calls (we describe this pattern below). When this was pronounced, it caused the appearance of silent gaps (Figure 4D8, call on right) or even of bipartite calls. DC was prominent around the frequency peak of many Class II Calls (Figure 4D10; see below). One bird uttered Class I Calls of intermediate duration that included very rapid modulations (Figure 5C2; see below).

FM assumed many forms. Sometimes it appeared simply as quasi-rhythmic fluctuations of the dominant frequency (Figure 5A1–A3). It also often was rhythmic, with small to large effects on the dominant frequency (Figure 5A4 and 5A5, respectively); some FM was based on compound units of repetition, as in plovers (Figure 5A6). Amplitude and frequency were inversely related, as seen in occurrences of strong FM (Figure 5B1), in the initial high frequency and low amplitude of many Class I Calls (Figure 5B2), and other call forms. Extremely rapid modulation was more common than in plovers, but was often slow enough so that modulations were visible (Figure 5B3). The rate of rapid modulation varied from moderate ($<$100 cps) to extremely fast (to approx. 1000 cps), with highest rates manifest as sidebands at some analytical settings (Watkins, 1967, Stein, 1968, Marler, 1969; Figure 5C1–C3).


A. Masked lapwing: Frequency changes within Class I Calls were diverse
Frequency (kHz)
A1
A2
A3
A4
A5
A6
mod. rate = 74 cps
70 cps
compound structure
L-14
L-18
L-24
L-25
L-3
L-26
0 200 400 600 800 1000 1200 1400 1600 1800 2000 2200 2400
B. Masked lapwing: Amplitude changes within Class I Calls were diverse
Relative amplitude
B1
B2
B3
FM and AM were closely (inversely) coupled in calls with strong FM
amplitude and frequency were inversely related in general
pulsing of the dominant frequency was common
(same call as A5)
mod. rate = 115, 137 cps
L-3
L-4
L-27
0 100 200 300 400 500 600 700 800 900 1000 1100 1200
C. Masked lapwing: Rate of rapid FM varied greatly within and across Class I Calls
C1
C2
50 ms
~165
DC
mod. rate ~370 cps
~600
to ~1000
to ~700
L-28
L-29
D. Masked lapwing: Nonlinear phenomena were common in Class I Calls
D1
D2
D3
D4
D5
FJ
DC often occurred at inflection points like frequency jumps
L-5
L-30
L-31
L-10
L-29
Time (ms)

Nonlinear phenomena were common. DC was present in many calls, often just around frequency maxima (Figure 5D1) but could occur anywhere, including across entire calls (Figure 5D2–D3). DC, rapid FM, or SHs commonly occurred at points of frequency change, such as at FJs (Figures 5D4, 6A4). Finally, SHs were common, could occur several times in a call, and often started or terminated abruptly, with switches from or to DC or tonality (Figure 5A). SH and DC often occurred together in calls (Figure 6A4–6A6).

Lapwings often uttered calls rapidly and rhythmically (Figure 6B–C). The lower limit to intervals between successive rapidly repeated calls was brief (the minimum was approx. 210 ms in Figure 6B; Kostoglou et al., 2022). In addition, trills occurred, with inter-call intervals much shorter than in Class I Call sequences (to 82 ms within trills of Class II Calls in Figure 6D).

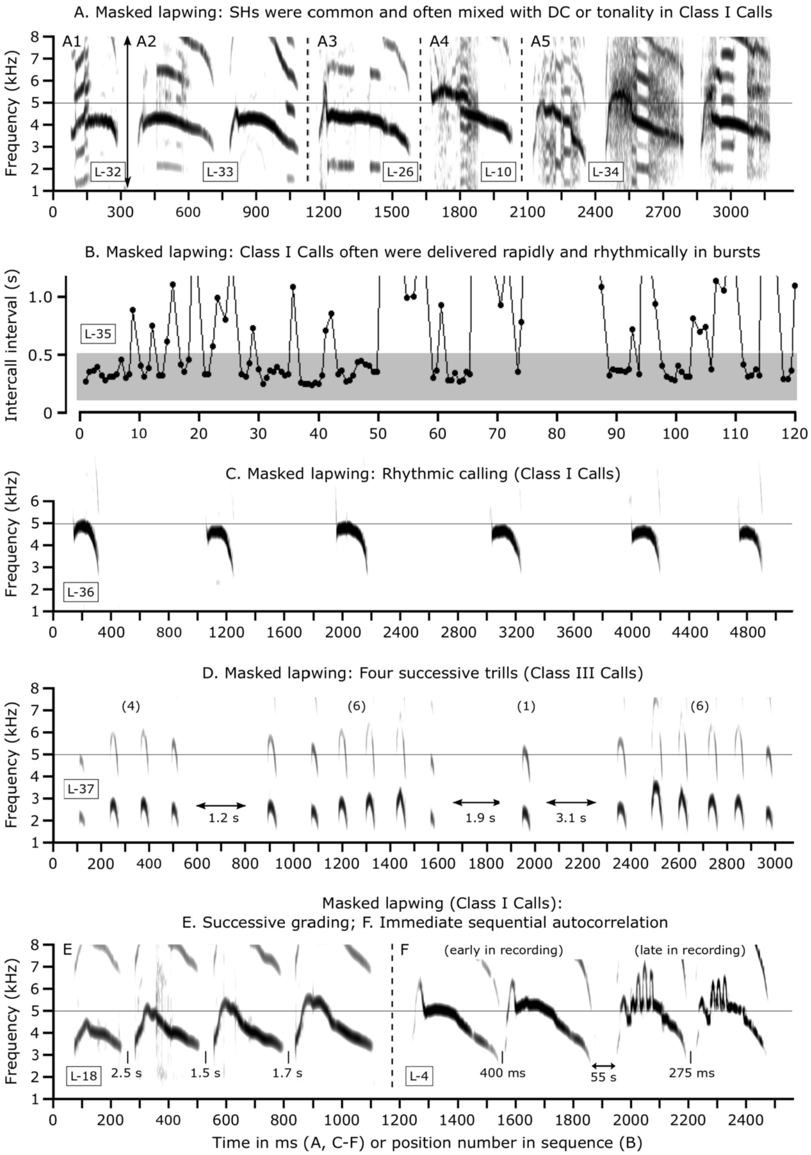
Successive calls often resembled one another closely (Figure 6C). In graded sequences, similarity across calls of course weakened over time (Figure 6E). Similarity between successive calls in general was often strong over small time scales, but structure could vary greatly over a recording: pairs of successive calls from early and late in one recording illustrate this point (Figure 6F).

### *3.3. Summary of similarities and differences in primary calls of the study species*

Recordings were dominated by a single class of call in each species. In plovers, this call showed pronounced FM with extensive DC. FM and DC were less common and more weakly expressed in lapwings, whose calls were mainly tonal. Calls of lapwings contained much more rapid modulation than

---

**Figure 5.** Changes in frequency and amplitude, and nonlinear phenomena, were diverse in calls of masked lapwing chicks. (A) Slow frequency modulation (FM) occurred in parts or all of many Class I Calls (A1–A3), but covered variable ranges in frequency and varied in repetition rate (A4–A5); sometimes FM was compound in structure (A6). (B) FM and AM were coupled in diverse Class I Calls; rapid FM could occur one to several times in calls (B3). (C) Rapid FM was expressed as sidebands at some analytical settings. (D) Deterministic chaos (DC) was common (D1–D3) and often occurred at frequency jumps (FJ: D4); sometimes frequency jumps showed no DC (D5). Calls in panels C1 and D4 were not successive and the intervals shown between them are arbitrary. Lapwing chick numbers (L-) denote different individuals, and are consistent within and across figures. Information on body mass, sex, and age (when known) is in the Appendix. The horizontal lines at 5 kHz are visual guides. Analysis settings are as stated in Methods, except number of points per analysis frame = 256 for A1–A6, 5B1, and 5B3, and 512 for C1–C2.


A. Masked lapwing: SHs were common and often mixed with DC or tonality in Class I Calls
Frequency (kHz)
A1
A2
A3
A4
A5
L-32
L-33
L-26
L-10
L-34
0 300 600 900 1200 1500 1800 2100 2400 2700 3000
B. Masked lapwing: Class I Calls often were delivered rapidly and rhythmically in bursts
Intercall interval (s)
L-35
0 0.5 1.0
0 10 20 30 40 50 60 70 80 90 100 110 120
C. Masked lapwing: Rhythmic calling (Class I Calls)
L-36
0 400 800 1200 1600 2000 2400 2800 3200 3600 4000 4400 4800
D. Masked lapwing: Four successive trills (Class III Calls)
(4)
(6)
(1)
(6)
L-37
1.2 s
1.9 s
3.1 s
0 200 400 600 800 1000 1200 1400 1600 1800 2000 2200 2400 2600 2800 3000
Masked lapwing (Class I Calls):
E. Successive grading; F. Immediate sequential autocorrelation
E
F
(early in recording)
(late in recording)
L-18
2.5 s
1.5 s
1.7 s
L-4
400 ms
55 s
275 ms
0 200 400 600 800 1000 1200 1400 1600 1800 2000 2200 2400
Time in ms (A, C-F) or position number in sequence (B)

those of plovers. A pulse preceded most of the primary calls of plovers; such introductory pulses were rare in lapwings.

Nonlinear phenomena were common in calls of both species but differed in prevalence and expression, e.g., DC was more common in plovers, whereas SHs were uncommon and weak and FJs did not occur. SHs were common and strong in lapwings, and FJs were common.

In both species, amplitude and frequency within calls were often inversely related, and lowest amplitude tended to occur when DC was strong. The inverse relationship was most apparent in calls with strong AM and FM. Successive calls (especially in bursts) tended to be similar to one another, but gradation occurred over call sequences, and calls at different times in recordings sometimes differed greatly.

We observed no trills in plovers but noted multiple occurrences in lapwing. Chicks of both species called erratically over time, interspersed with bursts of calls repeated rapidly and rhythmically.

We analyzed calls of a few other species from other sources (see Methods). Calls of a hand-held chick of Wilson's plover resembled those of red-capped plover strongly in some aspects: varied modulations; a pulse preceding some calls; DC; and series of calls uttered rhythmically and rapidly (Figure 7A; the smallest ICI was approx. 180 ms long). A FJ is also present in the sample (Figure 7A). As in many calls of red-capped plover, DC in Wilson's plover showed some vertical striations on spectrograms, presumably due to DC occurring at frequency maxima, as in red-capped plover), or it obscured frequency structure in part or entirely in some calls (Figure 7A, last two calls). We found no published analyses of chick distress calls in *Vanellus*

**Figure 6.** (A) Subharmonics (SHs) were common in Class I Calls of masked lapwing. (B) Class I Calls were uttered irregularly but often were given in bursts, with brief intervals between calls. (C) Part of a long sequence of rhythmically repeated Class I Calls (natural intervals shown). (D) Class II Calls were uttered singly or as brief trills (natural intervals within trills shown; intervals between successive calls noted). (E) Progressive changes across successive calls were common (intervals between calls noted). (F) Successive calls in bursts were similar to one another, but structure often changed over recordings (examples of pairs of successive calls separated by 55 s are shown; intervals between calls noted). Calls in A2 and A5 were not successive and then intervals shown between them are arbitrary. Lapwing chick numbers (L-) denote different individuals, and are consistent within and across figures. Information on body mass, sex, and age (when known) is in the Appendix. The horizontal lines at 5 kHz are visual guides. Analysis settings are as stated in Methods.

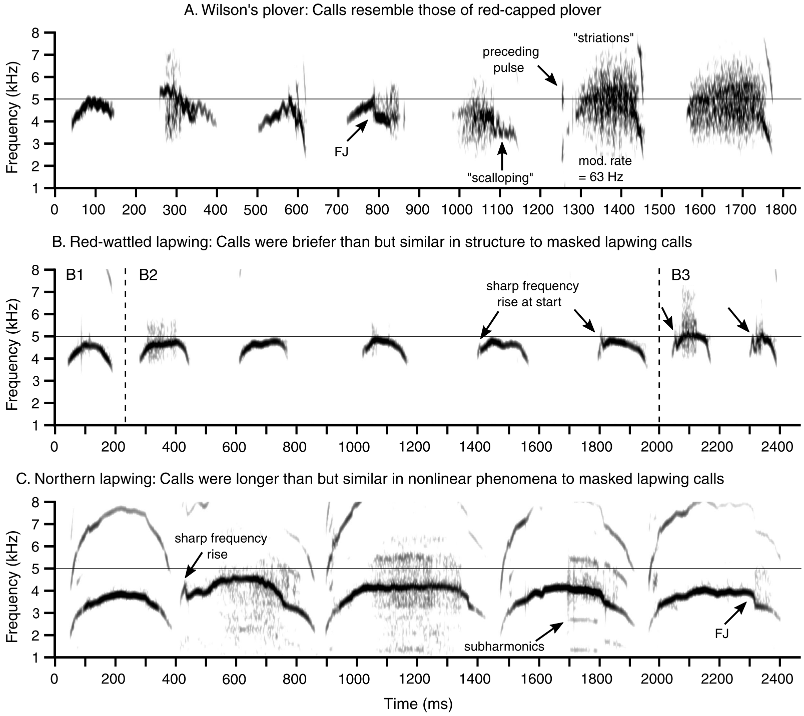


**Figure 7.** Distress calls of other plover and lapwing species. (A) Wilson's plover calls resembled those of red-capped plover in some key features (see text; note frequency jump, FJ). (B) Red-wattled lapwing: single call (B1), first five calls in 7-part series (B2); and second and third calls in other 7-part series (B3); natural intervals between calls are shown for B2 and B3. Note deterministic chaos and the sharp rise at the beginning of calls (arrows), as in masked lapwing. (C) Northern lapwing: five calls (not in sequence). Note deterministic chaos, subharmonics, and FJ with associated deterministic chaos (latter two marked by arrows). Calls in A and C were not successive and the intervals shown between them are arbitrary. Sources of sounds are provided in Methods. The horizontal lines at 5 kHz are visual guides. Analysis settings are as stated in Methods, except number of points per analysis frame = 512 for panels C and D.

species, but analyzed some from online videos. Calls of a hand-held red-wattled lapwing are briefer (<200 ms in Figure 7B; a maximum of 210 ms in the first and 250 ms in the second video of the species) and those of a young northern lapwing (not held in the hand) are longer (>400 ms in Figure 7C, >900 ms for one call) than in masked lapwing. Some calls of red-wattled lapwing started like most Class I Calls of masked lapwing, with a rapid rise to a frequency peak, followed by a dip (marked by arrows in Figure 7B), although the rises were weak; calls of northern lapwing started smoothly.

Calls of the newly hatched red-wattled lapwing chick in the second video of that species (spectrograms not included here) resembled the right-most call in Figure 7B2. Finally, both species expressed some DC (in agreement, Spencer (1935: p. 23) described "a wheezy but far-carrying *schwee*" call given by small northern lapwing chicks when separated from the parents), and several calls of northern lapwing had strong SHs. Both species uttered calls rhythmically, but intervals between successive calls (Inter-call Intervals, ICI) are not comparable because the northern lapwing was not in the hand (nevertheless, its calls were strikingly rhythmic in delivery: ICI median 2.59 s, minimum 1.55 s, $N = 58$); the shortest ICI of the red-wattled lapwing was approx. 125 ms (first video), substantially smaller than in masked lapwing.

## 4. Discussion

### *4.1. Structure of calls and calling*

We found strong differences in the structure of chick distress calls between red-capped plover and masked lapwing and high call variation within each species; one call form was dominant in each species but differed between them. Nonlinear phenomena also differed between species in their prevalence and expression. Simple forms of temporal patterning (e.g., successive grading) occurred in both species. We discuss these findings in this and the following section, and consider call functions in the last section.

Information on call structure in related species is needed to contextualize the species differences that we observed. Some published analyses are informative. The strong modulation and DC that characterized most calls of red-capped plover occur also in other *Charadrius* species. Furthermore, the pattern of periodic DC alternating with lower-frequency tonal sections (e.g., Fig 2A1, 2C1; 'scalloping') is clear in spectrograms of chick calls in mountain plover (*Ch. montanus*: Figure 3C of Graul, 1974) and piping plover (*Ch. melodus*: Figure 5J of Sung et al., 2005). One call of the latter species shows some smearing by DC (Figure 5J of Sung et al., 2005); the same is evident in killdeer (*Ch. vociferus*; Figure 1a of Heckenlively, 1972). One call of the latter species (Figure 5J of Sung et al., 2005) and two 'fearful calls' of a 4-day-old chick of little ringed plover (*Ch. dubius*, Figure 23 of Glutz von Blotzheim et al., 1975) are mainly frequency-descending and tonal, a call form that was present but uncommon in red-capped plover. None of three spectrograms of chick calls in lesser sand-plover (*Ch. mongolus*) in Gebauer & Nadler (1992) resembles those in our or other published studies. Also see notes on Wilson's plover call structure in Results.

In summary, some differences between calls of red-capped plover and masked lapwing seem to extend to higher taxonomic levels (i.e., *Charadrius* vs. *Vanellus*). More extensive recordings are needed to document similarities and differences properly, because of high intraspecific variation and because not all the recordings we examined were made in comparable circumstances (e.g., of the three videos examined, the chick was being handled while it called only in the first video of red-wattled lapwing). Certain call traits (e.g., high bandwidth, nonlinear phenomena) have been suggested as widespread acoustic adaptations to increase locatability of a calling bird (see Section 4.3); some of these traits differ substantially in presence and degree of expression between red-capped plover and masked lapwing.

Variation in distress calls, whether as a result of hand capture or in the presence of predators, also occurs among vireos, passerellid sparrows, and other passerines (Norris & Stamm, 1965; Stefanski & Falls, 1972; Ficken & Popp, 1996).

## *4.2. Call variation*

Variation in call structure occurred at multiple levels. Successive calls often expressed sequential grading, for example within trills (masked lapwing only) or in sequences (e.g., Figure 3B–C; Figure 6C–F). In general, this should enable listeners to track continuous changes in the caller's behavioural state or level of arousal (Schleidt, 1973). Short-term qualitative shifts (e.g., Figure 3D) could inform about sudden changes in the chick's motivational state. This is not possible for quantitative or qualitative differences across greater temporal scales, such as those resulting from the presence of different call traits across calls within recordings.

In each species, calls ranged from brief simple tonal calls to calls with multiple components, including nonlinearities. Such components were repeated or combined in various ways in different calls, which generated high variety across calls. Similar patterns of variation across calls due to recombination of distinctive call parts ('segments') have been observed and analysed in considerable detail in some birds and mammals (Miller & Murray, 1995; Fitch, 2012; Jansen et al., 2012; Hedwig et al., 2014; Mann, 2020; Mann et al., 2021).

Inter-call variation was limited in part by regularities in call structure, such as the presence of a preceding pulse in many red-capped plover calls, the rapid frequency rise at the start of many masked lapwing calls, and the generally negative association between amplitude and frequency in both species. Nevertheless, substantial complexity was expressed in many calls and varied in extent and nature across calls. We observed qualitative variation (at the level of different call classes) across recordings of one red-capped plover chick. Limits to variation in rate of calling are suggested by the uniform inter-call intervals in sequences of rapidly repeated calls (Figures 3A, 6B). Mechanisms of vocal control are central to acoustic variation, and vary both intraspecifically and across species and higher taxa (Goller & Riede, 2013; Goller, 2021; Goller et al., 2021). Mechanisms of vocalization in shorebirds are almost unknown (Riede et al., 2015), but differences within species seem likely considering the great variation in modulation rates that we observed.

Tikhonov & Fokin (1980) noted that shorebird chicks (including little ringed plover and common ringed plover *Ch. hiaticula*) gave 'discomfort calls' when chicks were cooled or hungry, or isolated from parents or siblings. Frequency bandwidth increased with 'intensity of emittance'; in addition, call sequences increased in duration and calling rate increased (intervals between calls decreased) as chicks were cooled (the reverse pattern was noted as chicks were warmed; op. cit.); a similar pattern has been reported for other species (Cramp, 1983; Rumpf & Tzschentke, 2010). Piersma (1996: p. 396) interpreted this kind of call as 'the juvenile version of adult contact call', which may apply to vocalizations of the northern lapwing described above (Figure 7C). These observations parallel ours on red-capped plover and masked lapwing, in which birds that appeared to be the most aroused or agitated gave loud rapidly repeated calls.

Features of call variation that may be important generally in the presence of a predator (next section) include gradual or sudden changes during call sequences, and acoustic variety, all of which are present in calls of red-capped plover and masked lapwing.

### *4.3. Call functions*

The structure of distress calls of red-capped plover and masked lapwing chicks agrees with a conventional picture of distress or mobbing sounds being adapted to be locatable by listeners: the calls are loud and repetitive, cover a broad frequency spectrum, and often are harsh in quality due to AM, FM, or nonlinear phenomena like DC (Högstedt, 1983; Davis, 1988; Brémond & Aubin, 1992; Marler, 2004; Blumstein, 2007). As noted, the calls also have the capacity to startle due to their variability over multiple time scales. Assessment of these traits as adaptations and understanding interspecific differences will require phylogenetic analyses and experimentation to identify intended receivers, determine effects of calls and call traits on receivers, and quantify the calls' active space. Behavioural observations also will be needed, and many anecdotal observations exist that can guide experimentation; e.g., Simmons (1955) noted that chick distress calls of little ringed plover and Kentish plover (*Ch. alexandrinus*) prompted nearby siblings to scatter and attracted parents, who engaged in distraction displays. In the only experiment ever conducted on a charadriid, Heckenlively (1972) observed that breeding adults (parents and other birds) were attracted to playbacks of chick distress calls and produced diversionary displays in response.

Chick distress calls of our study species shared some qualities but differed substantially in structure. Both species nest on the ground and have precocial young that are not fed by the parents. Therefore, both species are vulnerable in similar ways to diverse native and introduced predators, though both species have geographically vast and ecologically diverse ranges (Marchant & Higgins, 1993; del Hoyo et al., 2020; Wiersma et al., 2020). Furthermore, the study species differ in many ways that must be reflected in functions and adaptations of their calls, for example in body size, clutch size, patterns of parental investment, and many aspects of life history (see Material and methods; Thomas, 1969; Hobbs, 1972; Lees et al., 2013; Halimubieke et al., 2020); the same will undoubtedly apply also across the Charadriidae, in light of their diverse breeding ecology, mating systems, and parental care (Walters, 1980, 1982, 1984, 1990; Wiersma, 1996; Eberhart-Phillips, 2019; Stenzel & Page, 2019; Cerboncini et al., 2020). The study species also differ greatly and vary intraspecifically in breeding density (which determines how many breeding conspecific adult birds are within a call's active space), and in adult reactions to predators. For example, red-capped plovers are fairly timid, though approach potential predators and engage in distraction displays, whereas masked lapwings defend their nest or brood through distraction displays but also through mobbing by multiple conspecific adults, and they occasionally strike potential predators physically (including humans; Moffat, 1981; Cardilini et al., 2013; Lees et al., 2013; P. Temple-Smith in litt., 6 August 2021). In the present state of our meagre knowledge (even just about intended recipients), we cannot interpret acoustic differences between the species in relation to any of these factors.

Nonlinear phenomena are widespread in calls of vertebrates, including when animals are under stress (see Introduction). Distress calls that contain nonlinear phenomena may be more effective at inducing responses in conspecific or heterospecific listeners, in countering habituation in listeners, or facilitating individual identification (Fitch et al., 2002; Kasirova et al., 2005; Volodin et al., 2005; Volodina et al., 2006; Slaughter et al., 2013; Blesdoe et al., 2014). In shorebirds, nonlinear phenomena are present in distress calls (Adret, 2012; this study), but also occur in other circumstances and in other kinds of vocalizations in both chicks and adults (Nethersole-Thompson & Nethersole-Thompson, 1979; Miller, 1984, 1996; Ward, 1989; Byrkjedal & Thompson, 1998; Sung et al., 2005; Bergmann et al., 2008; Adret, 2012; Dragonetti et al., 2013a, b; Pieplow, 2019). Unlike in distress calls of chicks, nonlinear phenomena are stereotyped and occur at specific points in nuptial calls of breeding adults, such as frequency jumps in *Pluvialis* species (Connors, et al. 1993; Byrkjedal & Thompson, 1998) and semipalmated plover (*Ch. semipalmatus*; Sung et al., 2005), and deterministic chaos in stilt sandpiper (*Calidris himantopus*; Miller, 1983). Clearly, both the form of nonlinear phenomena and their predictability differ in communicative significance across such call types.

We recorded distress calls of red-capped plover and masked lapwing in the narrow circumstance of chicks being held in the hand. Therefore, variation in call traits or classes was not tied to different circumstances (vs. Green, 1975; Hicinbothom & Miller, 1999; Tallet et al., 2013). It seems most parsimonious to interpret variation as reflecting the emotional state of the caller, presumably to effect arousal in listeners (Bachorowski & Owren, 2003; Rendall & Owren, 2010; Briefer, 2020). We have avoided using the word ‘context’ until now because it is used in so many ways, and often only narrowly with reference to obvious and proximate physical or social factors. In contrast, in the formulation by Smith (1977, 1997, 2009), context includes all sources of information available to recipients that are outside the physical signal itself, including weather, time of day, sex, or age; and social factors such as dominance rank, kinship, or familiarity between sender and receiver. A pertinent example of the latter is the effect of social affiliation on emotional responses to distress calls in the cockatiel (*Nymphicus hollandicus*; Liévin-Bazin et al., 2018). Comparably detailed studies that address contextual factors (sensu Smith) will be needed to understand functions of distress calls in charadriids.

## Acknowledgements

For assistance and support for fieldwork, we thank Peter Dann (Phillip Island Nature Parks) and Rangers at the Point Cook Coastal Park (Russell Brooks, Mark Cullen, Ron Cuthbert, and Bernie McCarrick). For their generous help with varied aspects of the manuscript, including translations of Russian papers, technical advice on analyses, literature, interpretations, and personal observations, we thank Rachel Adams, Ricardo Cerboncini, David Černý, Ekaterina Ershova, Franz Goller, Janet Goosney, Don Kroodsma, Drew Rendall, Tobias Riede, Peter Temple-Smith, and Jeff Walters. Protocols were reviewed and approved by the Deakin University Animal Ethics Committee (approvals B01 2018, B11 2017, and B12 2017) and the Department of Environment, Land, Water and Planning (permits 10008437 and 10008619). This project was supported by The Holsworth Wildlife Research Endowment and The Ecological Society of Australia.

## References

Adret, P. (2012). Call development in captive-reared pied avocets, *Recurvirostra avosetta*. — J. Ornithol. 153: 535-546.

Amaya, J.P., Zufiaurre, E., Areta, J.I. & Abba, A.M. (2019). The weeping vocalization of the screaming hairy armadillo (*Chaetophractus vellerosus*), a distress call. — J. Mammal. 100: 1427-1435.

Andrew, R.J. (1969). The effects of testosterone on avian vocalizations. — In: Bird vocalizations: their relation to current problems in biology and psychology (Hinde, R.A., ed.). Cambridge University Press, Cambridge, p. 97-130.

Bachorowski, J.-A. & Owren, M.J. (2003). Sounds of emotion: production and perception of affect-related vocal acoustics. — Ann. N.Y. Acad. Sci. 1000: 244-265.

Baker, A.J., Pereira, S.L. & Paton, T.A. (2007). Phylogenetic relationships and divergence times of Charadriiformes genera: multigene evidence for the Cretaceous origin of at least 14 clades of shorebirds. — Biol. Lett. 3: 205-209.

Beckers, G.J.L. & ten Cate, C. (2006). Nonlinear phenomena and song evolution in *Streptopelia* doves. — Acta Zool. Sin. 52(supplement): 482-485.

Beer, C.G. (1977). What is a display? — Am. Zool. 17: 155-165.

Bergmann, H.-H., Helb, H.-W. & Baumann, S. (2008). Die Stimmen der Vögel Europas. — Aula-Verlag, Wiebelsheim.

Bergstrom, P.W. (1988). Breeding displays and vocalizations of Wilson's plovers. — Wilson Bull. 100: 36-49.

Berman, G.J. (2018). Measuring behavior across scales. — BMC Biol. 16: 23.

Blesdoe, E.K. & Blumstein, D.T. (2014). What is the sound of fear? Behavioral responses of white-crowned sparrows *Zonotrichia leucophrys* to synthesized nonlinear acoustic phenomena. — Curr. Zool. 60: 534-541.

Blumstein, D.T. (2007). The evolution, function, and meaning of marmot alarm communication. — Adv. Stud. Behav. 37: 371-401.

Bradbury, J.W. & Vehrencamp, S.L. (2011a). Principles of animal communication, 2nd edn. — Sinauer Associates, Sunderland, MA.

Bradbury, J.W. & Vehrencamp, S.L. (2011b). Principles of animal communication, second edition. — Web topic 2.4: Fourier analysis of animal sounds. Sinauer Associates, Sunderland, MA. Available online at http://sites.sinauer.com/animalcommunication2e/chapter02.04.01.html.

Brémond, J.-C. & Aubin, T. (1992). The role of amplitude modulation in distress-call recognition by the black-headed gull (*Larus ridibundus*). — Ethol. Ecol. Evol. 4: 187-191.

Briefer, E.F. (2020). Coding for 'dynamic' information: vocal expression of emotional arousal and valence in non-human animals. — In: Coding strategies in vertebrate acoustic communication (Aubin, T. & Mathevon, N., eds). Springer Nature, Cham, p. 137-162.

Byrkjedal, I. & Thompson, D. (1998). Tundra plovers: the Eurasian, Pacific and American golden plovers and grey plover. — Princeton University Press, Princeton, NJ.

Cambridge Dictionary (2021). — https://dictionary.cambridge.org/dictionary/english/modulation (accessed 3 June 2021).

Cardilini, A.P.A., Weston, M., Nimmo, G.D., Dann, P.M. & Sherman, C.D.H. (2013). Surviving in sprawling suburbs: suburban environments represent high quality breeding habitat for a widespread shorebird. — Landscape Urb. Plann. 115: 72-80.

Carro, M.E. & Fernández, G.J. (2021). Alarm calls of house wrens (*Troglodytes aedon bonariae*) elicit responses of conspecific and heterospecific species. — Behaviour 158: 829-847.

Cerboncini, R.A.S., Braga, T.V., Roper, J.J. & Passos, F.C. (2020). Southern lapwing *Vanellus chilensis* cooperative helpers at nests are older siblings. — Ibis 162: 227-231.

Černý, D. & Natale, R. (2021). Comprehensive taxon sampling and vetted fossils help clarify the time tree of shorebirds (Aves, Charadriiformes). — bioR$\chi$iv doi: https://doi.org/10.1101/2021.07.15.452585.

Collias, N.E. & Joos, M. (1953). The spectrographic analysis of sound signals of the domestic fowl. — Behaviour 5: 175-188.

Connors, P.G., McCaffery, B.J. & Maron, J.L. (1993). Speciation in golden-plovers, *Pluvialis dominica* and *P. fulva*: evidence from the breeding grounds. — Auk 110: 9-20.

Cramp, S. (ed.) (1983). Handbook of the birds of Europe the Middle East and North Africa. The birds of the western Palearctic, vol. 3: waders to gulls. — Oxford University Press, Oxford.

Davis Jr., W.E. (1988). Distress calls in birds: an avian enigma. — Bird Observ. 16: 205-210.

Davis Jr., W.E. (1991). Evolution of distress calls in birds: still an enigma. — Bird Observ. 19: 187-190.

del Hoyo, J., Wiersma, P., Kirwan, G.M. & Collar, N. (2020). Masked lapwing (*Vanellus miles*), version 1.0. — In: Birds of the world (Billerman, S.M., Keeney, B.K., Rodewald, P.G. & Schulenberg, T.S., eds). Cornell Lab of Ornithology, Ithaca, NY. Available online at https://doi.org/10.2173/bow.maslap1.01.

Digby, A., Bell, B.D. & Teal, P. (2013). Non-linear phenomena in little spotted kiwi calls. — Bioacoustics 23: 1-16.

Dragonetti, M., Caccamo, C., Corsi, F., Farsi, F., Giovacchini, P., Pollonara, E. & Giunchi, D. (2013a). The vocal repertoire of the Eurasian stone-curlew (*Burhinus oedicnemus*). — Wilson J. Ornithol. 125: 34-49.

Dragonetti, M., Caccamo, C., Pollonara, E., Baldaccini, N.E. & Giunchi, D. (2013b). A weak individual signature might not allow chick call recognition by parent stone curlews *Burhinus oedicnemus*. — Bioacoustics 22: 17-32.

Eberhart-Phillips, L.J. (2019). Plover breeding systems: diversity and evolutionary origins. — In: The population ecology and conservation of *Charadrius* plovers (Colwell, M.A. & Haig, S.M., eds). CRC Press, Boca Raton, FL, p. 65-88.

Ekanayake, K.B., Weston, M.A., Nimmo, D.G., Maguire, G.S., Endler, J.A. & Küpper, C. (2015). The bright incubate at night: sexual dichromatism and adaptive incubation division in an open-nesting shorebird. — Proc. Roy. Soc. Lond. B: Biol. Sci. 282: 20143026.

Ficken, M.S. & Popp, J. (1996). A comparative analysis of passerine mobbing calls. — Auk 113: 370-380.

Fischer, J., Wadewitz, P. & Hammerschmidt, K. (2016). Structural variability and communicative complexity in acoustic communication. — Anim. Behav. 134: 229-237.

Fitch, W.T., Neubauer, J. & Herzel, H. (2002). Calls out of chaos: the adaptive significance of nonlinear phenomena in mammalian vocal production. — Anim. Behav. 63: 407-418.

Fitch, W.T. (2012). Segmental structure in banded mongoose calls. — BMC Biol. 10: 98.

Francis, C.D. & Wilkins, M.R. (2021). Testing the strength and direction of selection on vocal frequency using metabolic scaling theory. — Ecosphere 12: e03733.

Gebauer, A. & Nadler, T. (1992). Verhalten und Stimme des Mongolenregenpfeifers *Charadrius mongolus*. — Limicola 6: 105-125.

Ginsberg, J.H. (2018). Acoustics — a textbook for engineers and physicists, vol. 1: fundamentals. — Springer International, Cham.

Glutz von Blotzheim, U.N., Bauer, K.M. & Bezzel, E. (eds) (1975). Handbuch der Vögel Mitteleuropas, Band 6: Charadriiformes (1. Teil). — Akademische Verlagsgesellschaft, Wiesbaden.

Goller, F. (2021). Vocal athletics — from birdsong production mechanisms to sexy songs. — Anim. Behav.: in press.

Goller, F. & Riede, T. (2013). Integrative physiology of fundamental frequency control in birds. — J. Phys.-Paris 107: 230-242.

Goller, F., Love, J. & Mindlin, G. (2021). Different frequency control mechanisms and the exploitation of frequency space in passerines. — Ecol. Evol. 11: 6569-6578.

Gottlieb, G. & Vandenbergh, J.G. (1968). Ontogeny of vocalization in duck and chick embryos. — J. Exp. Zool. 168: 307-326.

Gratto-Trevor, C.L. (2018). The North American bander's manual for shorebirds (Charadriiformes, suborder Charadrii). — North American Birding Council Publication Committee, Point Reyes Station, CA.

Graul, W.D. (1974). Vocalizations of the mountain plover. — Wilson Bull. 86: 221-229.

Green, S. & Marler, P. (1979). The analysis of animal communication. — In: Handbook of behavioral neurobiology, vol. 3: social behavior and communication (Marler, P. & Vandenbergh, J.G., eds). Plenum Press, New York, NY, p. 73-158.

Green, S. (1975). Variation of vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): a field study. — In: Primate behavior: developments in field and laboratory research, vol. 4 (Rosenblum, L.A., ed.). Academic Press, New York, NY, p. 1-102.

Greenewalt, C.H. (1968). Bird song: acoustics and physiology. — Smithsonian Institution Press, Washington, DC.

Halimubieke, N., Kupán, K., Valdebenito, J.O., Kubelka, V., Carmona-Isunza, M.C., Burgas, D., Catlin, D., St. Clair, J.H.J., Cohen, J., Figuerola, J., Yasué, M., Johnson, M., Mencarelli, M., Cruz-López, M., Stantial, M., Weston, M.A., Lloyd, P., Que, P., Montalvo, T., Bansal, U., McDonald, G.C., Liu, Y., Kosztolányi, A. & Székely, T. (2020). Successful breeding predicts divorce in plovers. — Sci. Rep. 10: 15576.

Heckenlively, D.B. (1972). Responses of adult killdeers to a downy young distress call. — Condor 74: 107-108.

Hedwig, D., Hammerschmidt, K., Mundry, R., Robbins, M.M. & Boesch, C. (2014). Acoustic structure and variation in mountain and western gorilla close calls: a syntactic approach. — Behaviour 151: 1091-1120.

Herborn, K.A., McElligott, A.G., Mitchell, M.A., Sandilands, V., Bradshaw, B. & Asher, L. (2020). Spectral entropy of early-life distress calls as an iceberg indicator of chicken welfare. — J. Roy. Soc. Interf. 17: 20200086.

Hicinbothom, G.M. & Miller, D.B. (1999). The influence of social context on the vocalizations of mallard ducklings (*Anas platyrhynchos*). — Bird Behav. 13: 47-57.

Hobbs, J.N. (1972). Breeding of red-capped dotterel at Fletcher's Lake, Dareton, NSW. — Emu 72: 121-125.

Högstedt, G. (1983). Adaptation unto death: function of fear screams. — Am. Nat. 121: 562-570.

James, F.C. & McCulloch, C.E. (1985). Data analysis and the design of experiments in ornithology. — In: Current ornithology, vol. 2 (Johnston, R.F., ed.). Plenum Press, New York, NY, p. 1-63.

Jansen, D.A.W.A.M., Cant, M.A. & Manser, M.B. (2012). Segmental concatenation of individual signatures and context cues in banded mongoose (*Mungos mungo*) close calls. — BMC Biol. 10: 97.

Kasirova, T.A., Volodin, I.A., Volodina, E.V., Kashentseva, T.A. & Beme, I.R. (2005). The structure and occurrence of biphonic calls in chicks of the Siberian crane (*Grus leucogeranus*). — Ornitologia 32: 97-104 (in Russian).

Klenova, A.V. & Kolesnikova, Y.A. (2013). Evidence for a non-gradual pattern of call development in auks (Alcidae, Charadriiformes). — J. Ornithol. 154: 705-716.

Klump, G.M. & Shalter, M.D. (1984). Acoustic behaviour of birds and mammals in the predator context. I. Factors affecting the structure of alarm signals. II. The functional significance and evolution of alarm signals. — Z. Tierpsychol. 66: 189-226.

Kostoglou, K.N., van Dongen, W.F.D., Lees, D., Maguire, G.S. & Weston, M.A. (2017). Acoustic cues from within the egg do not heighten depredation risk to shorebird clutches. — Behav. Ecol. 28: 811-817.

Kostoglou, K.N., van Dongen, W.F.D. & Weston, M.A. (2020). Parental defence in shorebirds is mediated by embryonic calling, ambient temperature and predator latency. — J. Ornithol. 161: 1153-1165.

Kostoglou, K.N., van Dongen, W.F.D. & Weston, M.A. (2021). Embryonic vocalizations mediate parental care in masked lapwings (*Vanellus miles*) but not red-capped plovers (*Charadrius ruficapillus*). — Ibis 164: 267-281.

Kostoglou, K.N., Miller, E.H., Weston, M.A. & Wilson, D.R. (2022). Vocal traits of shorebird chicks and their relationships with body mass and sex. — bioR$\chi$iv doi: https://biorxiv.org/cgi/content/short/2021.12.30.474581v1.

Lees, D., Sherman, C.D.H., Maguire, G.S., Dann, P., Cardilini, A.P.A. & Weston, M.A. (2013). Swooping in the suburbs; parental defence of an abundant aggressive urban bird against humans. — Animals 3: 754-766.

Lees, D., Sherman, C.D.H., Kostoglou, K., Tan, L.X.L., Maguire, G.S., Dann, P. & Weston, M.A. (2018). Plover parents care more for young of the opposite sex. — Behav. Ecol. 29: 933-938.

Lees, D., Schmidt, T., Sherman, C.D.H., Maguire, G.S., Dann, P. & Weston, M.A. (2019). Equitable chick survival in three species of the non-migratory shorebird despite species-specific sexual dimorphism of the young. — Animals 9: 271.

Liebezeit, J.R., Smith, P.A., Lanctot, R.B., Schekkerman, H., Tulp, I., Kendall, S.J., Tracy, D.M., Rodrigues, R.J., Meltofte, H., Robinson, J.A., Gratto-Trevor, C., McCaffery, B.J., Morse, J. & Zack, S.W. (2007). Assessing the development of shorebird eggs using the flotation method: species-specific and generalized regression models. — Condor 109(3): 2-47.

Liévin-Bazin, A., Pineaux, M., Clerc, O., Gahr, M., von Bayern, A.M.P. & Bovet, D. (2018). Emotional responses to conspecific distress calls are modulated by affiliation in cockatiels (*Nymphicus hollandicus*). — PLoS ONE 13: e0205314.

Mann, D.C. (2020). Segmental units in nonhuman animal vocalization as a window into meaning, structure, and the evolution of language. — Anim. Behav. Cogn. 7: 151-158.

Mann, D.C., Fitch, W.T., Tu, H.-W. & Hoeschele, M. (2021). Universal principles underlying segmental structures in parrot song and human speech. — Sci. Rep. 11: 776.

Marchant, S. & Higgins, P.J. (eds) (1993). Handbook of Australian, New Zealand & Antarctic birds, vol. 2: raptors to lapwings. — Oxford University Press, Melbourne, VIC.

Marler, P.R. (1969). Tonal quality of bird vocalizations. — In: Bird vocalizations: their relations to current problems in biology and psychology (Hinde, R.A., ed.). Cambridge University Press, Cambridge, p. 5-18.

Marler, P.R. (1976). Social organization, communication and graded signals: the chimpanzee and gorilla. — In: Growing points in ethology (Bateson, P.P.G. & Hinde, R.A., eds). Cambridge University Press, Cambridge, p. 239-280.

Marler, P.R. (2004). Bird calls: a cornucopia for communication. — In: Nature's music: the science of birdsong (Marler, P.R. & Slabbekoorn, H., eds). Elsevier Academic Press, Amsterdam, p. 132-177.

Marx, G., Leppelt, J. & Ellendorff, F. (2001). Vocalisation in chicks (*Gallus gallus dom.*) during stepwise social isolation. — Appl. Anim. Behav. Sci. 75: 61-74.

Miller, E.H. (1979). An approach to the analysis of graded vocalizations of birds. — Behav. Neur. Biol. 27: 25-38.

Miller, E.H. (1983). The structure of aerial displays in three species of Calidridinae (Scolopacidae). — Auk 100: 440-451.

Miller, E.H. (1984). Communication in breeding shorebirds. — In: Shorebirds: breeding behavior and populations (Burger, J. & Olla, B.L., eds). Plenum Press, New York, NY, p. 169-241.

Miller, E.H. (1996). Acoustic differentiation and speciation in shorebirds. — In: Ecology and evolution of acoustic communication in birds (Kroodsma, D.E. & Miller, E.H., eds). Cornell University Press, Ithaca, NY, p. 241-257.

Miller, E.H. & Baker, A.J. (2009). Antiquity of shorebird acoustic displays. — Auk 126: 454-459.

Miller, E.H. & Kochnev, A.A. (2021). Supplementary material for: ethology and behavioral ecology of the walrus (*Odobenus rosmarus*), with emphasis on communication and social behavior. — In: Ethology and behavioral ecology of otariids and the odobenid (Campagna, C. & Harcourt, R., eds). Springer Nature, Cham, p. 437-488.

Miller, E.H. & Murray, A.V. (1995). Structure, complexity, and organization of vocalizations in harp seal (*Phoca groenlandica*) pups. — In: Sensory systems of aquatic mammals (Kastelein, R.A., Thomas, J.A. & Nachtigall, P.E., eds). De Spil Publishers, Woerden, p. 237-264.

Mo, M. (2020). Nesting ecology of the masked lapwing *Vanellus miles novaehollandiae* at two peri-urban sites: breeding densities, nest characteristics, clutch sizes and hatching success. — Corella 44: 55-60.

Moffat, M. (1981). Aspects of the biology of the spur-winged plover (*Vanellus miles novaehollandiae* Stephens 1819). — M.Sc. thesis, Massey University, Palmerston North.

Morton, E.S. (1977). On the occurrence and significance of motivation-structural rules in some bird and mammal sounds. — Am. Nat. 111: 855-869.

Nethersole-Thompson, D. & Nethersole-Thompson, M. (1979). Greenshanks. — T. and A.D. Poyser, Berkhamsted.

Norris, R.A. & Stamm, D.D. (1965). Relative incidence of distress calls or "squeals" in mist-netted birds. — Bird-Banding 36: 83-88.

Pieplow, N. (2019). Peterson field guide to bird sounds of western North America. — Houghton Mifflin Harcourt, Boston, MA.

Piersma, T.A. (1996). Family Charadriidae (plovers). — In: Handbook of the birds of the world, vol. 3: hoatzin to auks (del Hoyo, J., Elliott, A. & Sargatal, J., eds). Lynx Edicions, Barcelona, p. 384-409.

Rendall, D. & Owren, M.J. (2010). Vocalizations as tools for influencing the affect and behavior of others. — In: Handbook of mammalian vocalization: an integrative neuroscience approach (Brudzynski, S.M., ed.). Academic Press, Amsterdam, p. 177-185.

Riede, T., Forstmeier, W., Kempenaers, B. & Goller, F. (2015). The functional morphology of male courtship displays in the pectoral sandpiper (Calidris melanotos). — Auk 132: 65-77.

Rohwer, S., Fretwell, S.D. & Tuckfield, R.C. (1976). Distress screams as a measure of kinship in birds. — Am. Midl. Nat. 96: 418-430.

Ruiz-Monachesi, M.R. & Labra, A. (2020). Complex distress calls sound frightening: the case of the weeping lizard. — Anim. Behav. 165: 71-77.

Rumpf, M. & Tzschentke, B. (2010). Perinatal acoustic communication in birds: why do birds vocalize in the egg?. — Open Ornithol. J. 3: 141-149.

Ryan, M.J. & Brenowitz, E.A. (1985). The role of body size, phylogeny, and ambient noise in the evolution of bird song. — Am. Nat. 126: 87-100.

Schleidt, W.M. (1973). Tonic communication: continual effects of discrete signs in animal communication systems. — J. Theor. Biol. 42: 359-386.

Simmons, K.E.L. (1955). The significance of voice in the behaviour of the little ringed and Kentish plovers. — Brit. Birds 48: 106-115.

Slaughter, I., Berlin, E.R., Bower, J.T. & Blumstein, D.T. (2013). A test of the nonlinearity hypothesis in great-tailed grackles (*Quiscalus mexicanus*). — Ethology 119: 309-315.

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. — In: Perspectives in ethology, vol. 12: communication (Owings, D.H., Beecher, M.D. & Thompson, N.S., eds). Plenum Press, New York, NY, p. 7-53.

Smith, W.J. (2009). Displays and messages in intraspecific communication. — Semiotica 1: 357-369.

Spencer, K.G. (1953). The lapwing in Britain. Some account of its distribution and behaviour, and of its rôle in dialect, folklore, and literature. — A. Brown & Sons, London.

Stefanski, R.A. & Falls, J.B. (1972). A study of distress calls of song, swamp, and white-throated sparrows (Aves: Fringillidae). II. Interspecific responses and properties used in recognition. — Can. J. Zool. 50: 1513-1525.

Stein, R.C. (1968). Modulation in bird sounds. — Auk 85: 229-243.

Stenzel, L.E. & Page, G.W. (2019). Breeding biology of *Charadrius* plovers. — In: The population ecology and conservation of *Charadrius* plovers (Colwell, M.A. & Haig, S.M., eds). CRC Press, Boca Raton, FL, p. 91-125.

Sung, H.-C., Miller, E.H. & Flemming, S.P. (2005). Breeding vocalizations of the piping plover (*Charadrius melodus*): structure, diversity, and repertoire organization. — Can. J. Zool. 83: 579-595.

Tallet, C., Linhart, P., Policht, R., Hammerschmidt, K., Šimeček, P., Kratinova, P. & Špinka, M. (2013). Encoding of situations in the vocal repertoire of piglets (*Sus scrofa*): a comparison of discrete and graded classifications. — PLoS ONE 8(8): e71841.

Tan, L.X.L., Buchanan, K.L., Maguire, G.S. & Weston, M.A. (2015). Cover, not caging, influences chronic physiological stress in a ground-nesting bird. — J. Avian Biol. 46: 482-488.

Temple-Smith, P.D.M. (1969). Some aspects of the biology of the spurwinged plover — *Vanellus miles novaehollandiae* (Stephens, 1819). — Honours B.Sc. thesis, University of Tasmania, Hobart, TAS.

Thomas, D.G. (1969). Breeding biology of the Australian spur-winged plover. — Emu 69: 81-102.

Tikhonov, A.V. & Fokin, S.Y. (1980). [Acoustic signalization and the behaviour of shorebirds in early ontogenesis 2. Signalization and the behaviour of nestlings] (in Russian). — Biol. Nauki 10: 45-54.

Tobias, J.A., Ottenburghs, J. & Pigot, A.L. (2020). Avian diversity: speciation, macroevolution, and ecological function. — Annu. Rev. Ecol. Evol. Syst. 51: 533-560.

Volodin, I.A., Volodina, E.V. & Filatova, O.A. (2005). [Structure, occurrence and functional significance of nonlinear phenomena in calls of terrestrial mammals] (in Russian). — Zh. Obshcheĭ Biol. 66: 346-362.

Volodina, E.V., Volodin, I.A., Isaeva, I.V. & Unck, C. (2006). Biphonation may function to enhance individual recognition in the dhole, *Cuon alpinus*. — Ethology 112: 815-825.

Walters, J.R. (1980). The evolution of parental behavior in lapwings. — Ph.D. thesis, University of Chicago, Chicago, IL.

Walters, J.R. (1982). Parental behavior in lapwings (Charadriidae) and its relationships with clutch sizes and mating systems. — Evolution 36: 1030-1040.

Walters, J.R. (1984). The evolution of parental behavior and clutch size in shorebirds. — In: Shorebirds: breeding behavior and populations (Burger, J. & Olla, B.L., eds). Plenum, New York, NY, p. 243-287.

Walters, J.R. (1990). Anti-predator behavior of lapwings: field evidence of discriminative abilities. — Wilson Bull. 102: 49-70.

Ward, D. (1989). Behaviour associated with breeding of crowned, blackwinged and lesser blackwinged plovers. — Ostrich 60: 141-150.

Watkins, W.A. (1967). The harmonic interval: fact or artifact in spectral analysis of pulse trains. — In: Marine bio-acoustics, vol. 2 (Tavolga, W.N., ed.). Pergamon Press, London, p. 15-42.

Wiersma, P., Kirwan, G.M. & Boesman, P.F.D. (2020). Red-capped plover (*Charadrius ruficapillus*), version 1.0. — In: Birds of the world (del Hoyo, J., Elliott, J., Sargatal, A., Christie, D.A. & de Juana, E., eds). Cornell Lab of Ornithology, Ithaca, NY. Available online at https://doi.org/10.2173/bow.recplo1.01.

Wiersma, P. (1996). Family Charadriidae [species accounts]. — In: Handbook of the birds of the world, vol. 3: hoatzin to auks (del Hoyo, J., Elliott, A. & Sargatal, J., eds). Lynx Edicions, Barcelona, p. 410-442.

Wilden, I., Herzel, H., Peters, G. & Tembrock, G. (1998). Subharmonics, biphonation, and deterministic chaos in mammal vocalization. — Bioacoustics 9: 171-196.

Wiley, R.H. (2015). Noise matters: the evolution of communication. — Harvard University Press, Cambridge, MA.

Zuberbühler, K. (2009). Survivor signals: the biology and psychology of animal alarm calling. — Adv. Stud. Behav. 40: 277-322.

## Appendix

### *A.1. Summary of sex and body mass of red-capped plover ("plover") and masked lapwing ("lapwing") chicks whose calls are shown in figures in this paper.*

The following information is summarized as: (1) chick reference number (P-1, L-1, etc., as indicated on the figures); (2) figures and panels in which the chicks' calls are shown; (3) sex of the chick (F = female, M = male, U = unknown); and (4) body mass (in grams). Chicks measured on the nest (i.e., 0–1 day of age) are underlined.

Over all recordings, plover chicks averaged 9.9 g in body mass (median 8.4; range 2.6–21.8). Six chicks weighed at the nest (i.e., 0–1 day of age) weighed 4.2 ± 1.06 (SD) g (average and median were identical; range 2.6–5.5); in their large sample of newly hatched chicks, Lees et al. (2019) estimated body mass as 5.3 ± 0.06 g. Growth up to 2 weeks of age is undocumented for this species, and varies greatly (range approx. 13–28) after that (up to approx. 4 weeks of age; Lees et al. 2019).

Recorded lapwing chicks averaged 42.9 g in body mass (median 29.0; range 7.4–209). Those figures correspond to chicks ranging from newly hatched to about 5-7 weeks of age (average approx. 2 weeks; median approx. 1 week; Temple-Smith, 1969; Thomas, 1969; Moffat, 1981). Thirteen chicks weighed at the nest averaged 20.8 ± 2.67 g in body mass (median 21.5; range 15.3–24.3), compared with 20.8 ± 0.15 in the study by Lees et al. (2019).

We recorded six plovers and 14 lapwings (one of which was not weighed) aged 0–1 day. Those with calls analyzed in this paper (three plovers; three lapwings) are underlined. We recaptured one plover chick (P-12) at the age of 6–7 days.

Plovers: P-1: 1A1, 3E; M; 9.1 g. P-2: 1A2, 1C1, 1C3, 2C3; M; 4.2 g. P-3: 1A3, 1C1; M; 4.5 g. P-4: 1B1; F; 19.7 g. P-5: 1B2; M; 19.7 g. P-6: 1B3, 3A, 3B2; M; 11.3 g. P-7: 1B4, 2C4; M; 4.6 g. P-8: 1B5; M; 5.0 g. P-9: 1C2, 2D4; M; 4.8 g. P-10: 1C4, 1C5, 1C6, 2A1, 3B4; M; 3.6 g. P-11: 2A2; F; 5.5. g. P-12: 2A3; M; 4.8 g. P-13: 2B1; U; 5.7 g. P-14: 2B2; M; 14.8 g. P-15: 2B3, 3B1, 3C; M; 4.2 g. P-16: 2C1; M; 6.3 g. P-17; 2C2: F; 5.3 g. P-18: 2D1, 3B3; M; 6.5 g. P-19: 2D2; F; 4.6 g. P-20: 2D3; F; 3.9 g. P-21: 2D5; M; 3.8 g; 0 d. P-22: 3D; M; 5.1 g.

Lapwings: L-1: 4A1; F; 21.2 g. L-2: 4A2, 5B2; M; 18.2 g. L-3: 4A3, 5A5, 5B1; U; 70.0 g. L-4: 4A4, 4B2; M; 19.2 g. L-5: 4A5, 5C1; F; 18.5 g. L-6: 4A6; M; 19.2 g. L-7: 4B1; M; 48.3 g. L-8: 4B2; M; unknown mass. L-9: 4B3; F; 44.6 g. L-10: 4B4, 5D4, 6A4; M; 83.0 g. L-11: 4B5; F; 39.6 g. L-12: 4B6; M; 49.7 g. L-13: 4C1; M; 32.5 g. L-14: 4C2, 5A1; F; 23.9 g. L-15: 4C3; F; 29.0 g. L-16: 4C4; F; 23.9 g. L-17: 4C5; F; 97.0 g. L-18: 4C6, 5A2, 6E; M; 22.4 g. L-19: 4D1, 4D3, 4D7, 4D9; F; 15.2. L-20: 4D2, 4D10; M; 22.0 g. L-21: 4D4, 4D6; M; 20.8 g. L-22: 4D5; F; 20.7 g. L-23: 4D8; F; 45.4. L-24: 5A3; F; 22.5 g. L-25: 5A4; F; 53.9 g. L-26: 5A6, 6A3; F; 133.0 g. L-27: 5B3; M; 31.4 g. L-28: 5C1; M; 17.0 g. L-29: 5C2, 5D5; M; 44.9 g. L-30: 5D2; F; 20.1 g. L-31: 5D3; M; 19.5 g. L-32: 6A1; M; 56.1 g. L-33: 6A2; M; 22.3 g. L-34: 6A5; F; 15.3 g. L-35: 6B; M; 36.0 g. L-36: 6C; M; 45.2 g. L-37: 6D; M; 18.5 g.