

1 **Citation:**

2 **Miller EH, Kostoglou KN, Wilson DR, Weston MA (2022) Anatomy of avian distress calls: structure,**
3 **variation, and complexity in two species of shorebird (Aves: Charadrii). *Behaviour*, 159: 699–733. doi:**
4 **10.1163/1568539X-bja10147**

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

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21 Short title: Complexity and variation in shorebird distress calls

22 **Summary**

23

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

36

37 **Keywords**

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

40 1. Introduction

41

42 Many animals utter distinctive calls when threatened or captured by a predator. Such so-called
43 “distress calls” are widespread and can be strikingly similar in structure across distantly related
44 forms, including lizards, mammals, and birds (Davis, 1988, 1991; Marler, 2004; Amaya et al.,
45 2019; Ruiz-Monachesi & Labra, 2020). Diverse proximate and ultimate functions of distress
46 calls have been proposed. Calls may serve to startle the predator; attract other predators that
47 compete with the first one and enable the caller to escape; or attract individuals of the same or
48 different species that attack, mob, or distract the predator (Högstedt, 1983; Klump & Shalter,
49 1984; Davis, 1991; Marler, 2004; Zuberbühler, 2009; Carro & Fernández, 2021). These varied
50 possibilities are paralleled by varied interpretations of how distress calls evolve, for example
51 through natural selection acting directly on the vocalizing individual, altruistic selection, or kin
52 selection (Rohwer et al., 1976; Davis, 1991). Testing these hypotheses will require knowledge
53 about natural history and behaviour of each species, and determination of the identity of the
54 intended receiver(s) and, correspondingly, about the distance(s) over which distress calls are
55 adapted for transmission (i.e., the active space -- e.g., short distances for nearby siblings or
56 longer distances to reach parents or other adult birds in the vicinity). Transmission distance is
57 important for understanding structural adaptations in calls because sounds change over distance
58 (e.g., in amplitude and frequency spectrum), hence acoustic displays differ in structure between
59 those adapted for communication over short vs. long distances (Morton, 1977; Marler, 2004;
60 Bradbury & Vehrencamp, 2011a; Wiley, 2015). It follows that information about the structure of
61 distress calls is essential for testing adaptive or functional hypotheses and interpreting
62 experimental results. Knowledge about structure also is needed above the level of individual

63 calls, such as how calls are patterned over call sequences. For example, distress calls are repeated
64 rapidly in many birds (Davis, 1988; Marler, 2004), presumably because the property of rapid
65 repetition is adaptive. Other properties of call sequences (e.g., short-term variety, which may
66 startle a predator) also may be adaptive, hence should be included in descriptions.

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

76 We studied sound recordings of chicks made opportunistically during field research on the
77 red-capped plover (*Charadrius ruficapillus*) and the southern subspecies of masked lapwing
78 (*Vanellus miles novaehollandiae*; del Hoyo et al., 2020; Kostoglou, van Dongen et al., 2017;
79 2020, 2021; Kostoglou, Miller et al., 2022; Lees et al., 2018, 2019; “plovers” and “lapwings”
80 hereafter). We analyzed relationships of acoustic structure to sex and body size based on several
81 quantitative traits (Kostoglou, Miller et al., 2022). Here we provide an in-depth qualitative
82 analysis of calls. Knowledge of acoustic structure is crucial to many areas of investigation. The
83 importance of baseline descriptions can be illustrated with a publication that is nearly 70 years
84 old, on calls of the domestic fowl (*Gallus gallus*; Collias & Joos, 1953): that publication has

85 been cited nearly 400 times in a broad range of basic and applied research areas, including in
86 recent publications (e.g., Herborn et al., 2020).

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

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

106 We anticipated that our findings would support several established trends. First, distress calls
107 would be brief, relatively simple in structure, and structurally variable, as in chicks of other

108 precocial species (Collias & Joos, 1953; Marx et al., 2001; Adret, 2012; Dragonetti et al., 2013a,
109 b). Nevertheless, nonlinear phenomena (resulting from desynchronization of sound-production
110 mechanisms in the vocal tract) are apparent in some accounts (Dragonetti et al., 2013b), so we
111 expected to observe them also. Second, we expected to find strong similarities between calls of
112 the study species. This expectation was based on the observation that the structure and
113 repertoires of acoustic displays in shorebirds have evolved slowly, even for nuptial displays that
114 commonly evolve rapidly through social selection (Miller & Baker, 2009; Tobias et al., 2020).
115 Therefore, we anticipated that call structure and repertoires would be similar between the study
116 species, particularly for young chicks (Gottlieb & Vandenberg, 1968; Klenova & Koleshnikova,
117 2013). Modern estimates suggest more recent divergence times than in past studies (e.g. Baker et
118 al., 2007), but nevertheless the two clades that include our study species are quite old (the clades
119 diverged from one another in the Oligocene, ~30+ mya; Černý & Natale, 2021). We could not
120 make detailed predictions about the nature of vocal divergence because very few analyses of
121 chick calls in *Charadrius* and *Vanellus* species are available. Our third expectation was that the
122 species' calls would differ in frequency traits because the species differ so greatly in body size
123 (adult masked lapwings weigh about ten times as much as red-capped plovers; see below), and
124 frequency and body mass tend to be inversely related in birds (Ryan & Brenowitz, 1985; Francis
125 & Wilkins, 2021). We address only the first two expectations in this paper; the third is analyzed
126 in Kostoglou, Miller et al. (2022).

127 Below we describe call structure and variation for each species. First, we treat traits, trait
128 variation, and trait organization at the level of the individual call. Then we describe aspects of
129 organization above the level of the call, including intergradation across successive calls (a

130 pattern variously referred to as drift, sequential or adjacent grading, etc.; Andrew, 1969; Marler,
131 1976; Green & Marler, 1979; Miller, 1979).

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

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142

143 **2. Material and methods**

144

145 The following summary is based on Temple-Smith (1969), Moffat (1981), Marchant & Higgins
146 (1993), del Hoyo et al. (2020), Mo (2020), Wiersma et al. (2020), and personal observations.

147 Red-capped plovers commonly nest on coastal sandy or shell beaches, and bare areas at inland
148 wetlands or anthropogenic habitats (e.g., sewage ponds), etc. (details in Wiersma et al., 2020). In
149 Australia, they breed over an extended period that encompasses the austral summer (December-
150 February). They nest in open habitat or under low vegetation; clutch size is 1-2. The species is
151 small (body mass, 35–40 g) and sexually dichromatic (males have bright red heads, and females
152 generally have duller orange heads) but the sexes are similar in body size. Parental care is shared

153 more-or-less equally between the parents, though females tend to incubate by day and to rear
154 female-dominated broods (Ekanayake et al., 2015; Lees et al., 2018). We studied plovers from
155 October 2017 to March 2018 in Cheetham Wetlands, Point Cook, Australia (37°54' S 144° 47'
156 E), where nests are protected by predator-exclusion cages (Tan et al., 2015).

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

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

175 (Appendix), we report body mass and some ages for chicks whose calls are analyzed
176 spectrographically in this paper.

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

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

189 We normalized recordings at 24-bit resolution with Audacity 3.0.2 (audacityteam.org). We
190 inspected recordings with seewave 2.1.6 (rug.mnhn.fr/seewave), Praat (praat6142, 16-bit edition;
191 <https://www.fon.hum.uva.nl/praat/>), or Raven Pro 1.6 (ravensoundsoftware.com/software/raven-
192 pro/). We prepared illustrations in Inkscape 1.0.2 (inkscape.org) from waveforms and
193 spectrograms produced in Raven Pro. We used the following analytical settings for
194 spectrograms, except as indicated in some figure legends: Blackman window; 324 sample points
195 (= 7.35 ms); 89.8% overlap; and DFT size, 512 (= 86.1 Hz). We used a few different time and
196 frequency scales to accommodate variation across calls (e.g., calls of low vs. high frequency) and
197 to serve purposes of different figures.

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

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

218

219

220 **3. Results**

221

222 *3.1. Red-capped plover*

223

224 FM was prominent in most calls but varied greatly in expression. For convenience in description,
225 we considered calls with periodicity (AM or FM, even when the latter was obscured due to
226 deterministic chaos [see further]) to be a single class (*Class I Calls*). These were the commonest
227 kind of call in our sample. Periodicity was expressed most simply as FM (Figures 1-3). Usually
228 calls with FM also had extensive broadband “noise”, produced by the nonlinear phenomenon of
229 deterministic chaos (DC hereafter; Wilden et al., 1998; Beckers & ten Cate, 2006; Digby et al.,
230 2013).

231 The frequency range of *Class I Calls* varied greatly because: (1) the general trajectory of
232 frequency spanned different frequency ranges across calls (Figure 1A1-A3); and (2) the
233 frequency range covered by FM fluctuations varied greatly: compare calls in Figure 1A2 (right),
234 1A3, and 1B.

235 The rate of modulation varied within and across calls. It often declined over a call (e.g.,
236 Figure 1B3), and varied about 4-fold across calls (about 21-86 cps [cycles per second]) for calls
237 in Figure 1B. Its temporal pattern sometimes was slightly irregular (Figure 1C1-C2) or complex
238 (compound modulations in Figure 1C3). FM occurred throughout or at different places within
239 calls (Figure 1C4-C6). Calls with lengthened frequency maxima or minima of course had slower
240 repetition rates (see further). Very rapid modulation was rare, and occurred as discrete sequences
241 once or several times within calls (Figure 1C4 call on right). A single sharp pulse (sometimes
242 several pulses) preceded most *Class I Calls* (Figure 2A2, 2B1, B3, 2C3).

243 DC was expressed most strongly at frequency peaks in calls with periodicity (e.g., Figure
244 2A1). Sometimes DC obscured frequency structure or periodicity partly or completely (Figure
245 2A2-A3). A striking feature of frequency and DC was their association with one another and
246 with amplitude. Amplitude peaks in the waveform were associated weakly with minimal
247 frequency in calls that lacked DC (Figure 2B1; first part of Figure 2B2). However, that
248 relationship was pronounced when ~rhythmic DC was present because DC was associated so
249 strongly with low amplitude (Figure 2B2-B3). This imparted a vertically striated pattern on
250 spectrograms to all or parts of calls with periodicity (Figure 2A-A2, 2B3, C1, etc.). The striations
251 revealed the presence and enabled measurement of rates of periodicity even when frequency
252 peaks were not visible.

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

257 Both DC and non-DC portions of periodicity varied in duration in *Class I Calls*. The low-
258 frequency tonal segments (i.e., consisting of the fundamental frequency and various harmonics)
259 between successive rhythmically repeated DC segments of calls often lengthened, leading to
260 increased temporal separation of DC segments (e.g., both calls in Figure 2A1). The degree of
261 lengthening varied within and across calls (Figure 2C). Call doublets, triplets, etc., were
262 suggested when frequency minima were lengthened substantially and separated by sharp (e.g.,
263 first call in Figure 2C2) or low-amplitude (e.g., second call in Figure 2C2) peaks. Despite the
264 structural commonality between *Class I Calls* and such calls, we recognized the latter (e.g.,
265 Figure 2C2-C3, Figure 3D [first four and last two calls]) as a different call class (*Class II*).

266 The acoustic traits described above, in combination with temporal breaks, pulses,
267 combinations of different patterns of periodicity, etc., produced highly varied calls (Figure 2D).
268 Two nonlinear phenomena other than DC are common in bird vocalizations: subharmonics and
269 frequency jumps (SH and FJ, respectively; Wilden et al., 1998). In plover calls, SH occurred
270 fairly often but usually was weak (Figure 2D1); we observed FJs.

271 The temporal pattern of delivery of *Class I Calls* varied from ~rhythmic repetition in short to
272 long bursts (Figure 3A-C) to single calls uttered irregularly. We observed no kind of call that we
273 could consider as a trill (e.g., as couplets, triplets, or longer series). The interval between rapidly
274 repeated *Class I Calls* sometimes was very brief (~110 ms in Figure 3A; < 80 ms in some
275 sequences: Kostoglou, Miller et al., 2022). On a small temporal scale, successive *Class I Calls* in
276 bursts were similar to one another (Figure 3B), but gradual variation over sequences was
277 common (e.g., in call duration, inter-call interval, and frequency; Figure 3C). The tendency to
278 utter similar calls in sequence even characterized slowly repeated calls; an example for *Class II*
279 *Calls* (with a switch to other sorts of calls within the sequence) is shown in Figure 3D. We
280 observed a kind of brief tonal call only in one recording (*Class III Calls*; Figure 3E). It occurred
281 singly or in rhythmic sequences. These calls were in the second of three sound recordings made
282 at different ages for a single chick; *Class I Calls* dominated that chick's first and third
283 recordings.

284

285 3.2. *Masked lapwing*

286

287 Most lapwing calls were predominantly tonal. The simple structure of a common form included a
288 brief rapid rise to a frequency maximum (sometimes to > 8 kHz), followed by a gradual decline

289 in frequency (Figure 4A1-A2, 4A6), ranging to a sharp drop followed by a gradual decline
290 (Figure 4A). This simple form was commonly given by birds in the hand (Figure 4A1-A5) and
291 also was the main form of call uttered by chicks held in bags (Figure 4A6). It varied greatly and
292 graded into simpler calls (Figure 4C). We considered these together as *Class I Calls*; as for
293 plovers, we recognize that they may not constitute a natural structural class.

294 *Class I Calls* rarely were preceded by a pulse, and varied greatly at the start. The initial
295 frequency peak ranged over > 4 kHz across calls, and varied from being sharply peaked (e.g.,
296 Figure 4A3-A5, 4B1, 4B3) to slightly or even extensively rounded (Figure 4A1-A2, 4A6, 4B2,
297 4B6). The introductory peak ranged from high (some to > 8 kHz) to only slightly higher than the
298 remainder of the call (Figure 4A1, 4A3, 4C1-C2); sometimes no peak occurred (Figure 4C3-C6).
299 Most *Class I Calls* were strongly asymmetric across their course because frequency rose quickly
300 at or near the beginning of the call, then declined more slowly. Asymmetry to some degree was
301 almost universal however: weak asymmetry can be seen in Figure 4C, and extremely weak
302 asymmetry in Figure 4C4-C6. *Class I Calls* varied in other ways as well, in frequency range,
303 duration, the trajectory of the dominant frequency, variations in the dominant frequency, etc.
304 (Figure 4). We discuss these and other aspects of *Class I Calls* below.

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

308 We included some brief calls within *Class I Calls* (e.g., Figure 4C5-C6) but recognized
309 others as a distinct class. *Class II Calls* were extremely brief (most < 100 ms in duration) and
310 were characterized by a rapid rise in frequency to a peak, followed by a slightly slower
311 frequency decline to the end (Figure 4D). Frequency changes around the peak ranged from

312 gradual (Figure 4D1-D2) to sudden (i.e., the peak was sharp; Figure 4D8-D9). Frequency around
313 the peak was lowest in amplitude, as for *Class I Calls* (we describe this pattern below). When
314 this was pronounced, it caused the appearance of silent gaps (Figure 4D8, call on right) or even
315 of bipartite calls. DC was prominent around the frequency peak of many *Class II Calls* (Figure
316 4D10; see below). One bird uttered *Class I Calls* of intermediate duration that included very
317 rapid modulations (Figure 5C2; see below).

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

328 Nonlinear phenomena were common. DC was present in many calls, often just around
329 frequency maxima (Figure 5D1) but could occur anywhere, including across entire calls (Figure
330 5D2-D3). DC, rapid FM, or SHs commonly occurred at points of frequency change, such as at
331 FJs (Figures 5D4, 6A4). Finally, SHs were common, could occur several times in a call, and
332 often started or terminated abruptly, with switches from or to DC or tonality (Figure 6A). SH and
333 DC often occurred together in calls (Figure 6A4-A6).

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

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

343

344 *3.3. Summary of similarities and differences in primary calls of the study species*

345

346 Recordings were dominated by a single class of call in each species. In plovers, this call showed
347 pronounced FM with extensive DC. FM and DC were less common and more weakly expressed
348 in lapwings, whose calls were mainly tonal. Calls of lapwings contained much more rapid
349 modulation than those of plovers. A pulse preceded most of the primary calls of plovers; such
350 introductory pulses were rare in lapwings.

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

354 In both species, amplitude and frequency within calls were often inversely related, and
355 lowest amplitude tended to occur when DC was strong. The inverse relationship was most
356 apparent in calls with strong AM and FM. Successive calls (especially in bursts) tended to be

357 similar to one another, but gradation occurred over call sequences, and calls at different times in
358 recordings sometimes differed greatly.

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

362 We found no published analyses of chick distress calls in *Vanellus* species, but analyzed
363 some from online videos (see Methods). Calls of a hand-held red-wattled lapwing are briefer (<
364 200 ms in Figure 7B; a maximum of 210 ms in the first and 250 ms in the second video of the
365 species) and those of a young northern lapwing (not held in the hand) are longer (> 400 ms in
366 Figure 7C, > 900 ms for one call) than in masked lapwing. Some calls of red-wattled lapwing
367 started like most *Class I Calls* of masked lapwing, with a rapid rise to a frequency peak,
368 followed by a dip (marked by arrows in Figure 7B), although the rises were weak; calls of
369 northern lapwing started smoothly. Calls of the newly hatched red-wattled lapwing chick in the
370 second video of that species (spectrograms not included here) resembled the right-most call in
371 Figure 7B2. Finally, both species expressed some DC (in agreement, Spencer [1935, p. 23]
372 described “a wheezy but far-carrying *schwee*“ call given by small northern lapwing chicks when
373 separated from the parents), and several calls of northern lapwing had strong SHs. Both species
374 uttered calls rhythmically, but intervals between successive calls (Inter-call Intervals, ICI) are not
375 comparable because the northern lapwing was not in the hand (nevertheless, its calls were
376 strikingly rhythmic in delivery: ICI median, 2.59 s, minimum 1.55 s, $N = 58$); the shortest ICI of
377 the red-wattled lapwing was ~125 ms (first video), substantially smaller than in masked lapwing.

378

379

380 4. Discussion

381

382 4.1. Structure of calls and calling

383

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

390 Information on call structure in related species is needed to contextualize the species
391 differences that we observed. Some published analyses are informative. The strong modulation
392 and DC that characterized most calls of red-capped plover occur also in other *Charadrius*
393 species. Furthermore, the pattern of periodic DC alternating with lower-frequency tonal sections
394 (e.g., Fig 2A1, 2C1; “scalloping”) is clear in spectrograms of chick calls in Mountain Plover (*Ch.*
395 *montanus*: Figure 3C of Graul, 1974) and piping plover (*Ch. melodus*: Figure 5J of Sung et al.,
396 2005). One call of the latter species shows some smearing by DC (ibid.); the same is evident in
397 killdeer (*Ch. vociferus*; Figure 1a of Heckenlively, 1972). One call of the latter species (ibid.)
398 and two “fearful calls” of a 4-day-old chick of Little Ringed Plover (*Ch. dubius*, Figure 23 of
399 Glutz et al., 1975) are mainly frequency-descending and tonal, a call form that was present but
400 uncommon in red-capped plover. None of three spectrograms of chick calls in lesser sand-plover
401 (*Ch. mongolus*) in Gebauer & Nadler (1992) resembles those in our or other published studies.
402 Finally, possible DC is shown in a poor spectrogram of a hand-held chick of Wilson’s plover

403 (*Ch. wilsonia*; Figure 4J of Bergstrom, 1988); fortunately, that researcher deposited his
404 recordings in the Macaulay Library so we were able to analyze them.

405 Bergstrom's calls of a hand-held chick of Wilson's plover resembled those of red-capped
406 plover strongly in some aspects: varied modulations; a FJ; a pulse preceding some calls; DC; and
407 series of calls uttered rhythmically and rapidly (Figure 7A; the smallest ICI was ~180 ms long).
408 As in many calls of red-capped plover, DC in Wilson's plover sometimes showed vertical
409 striations on spectrograms ("striations"; presumably due to DC occurring at frequency maxima,
410 as in red-capped plover), or it obscured frequency structure in part or entirely in many calls
411 (Figure 7A, last two calls).

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

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

424

425 *4.2. Call variation*

426

427 Variation in call structure occurred at multiple levels. Successive calls often expressed sequential
428 grading, for example within trills (masked lapwing only) or in sequences (e.g., Figure 3B-C;
429 Figure 6C-F). In general, this should enable listeners to track continuous changes in the caller's
430 behavioural state or level of arousal (Schleidt, 1973). Short-term qualitative shifts (e.g., Figure
431 3D) could inform about sudden changes in the chick's motivational state. This is not possible for
432 quantitative or qualitative differences across greater temporal scales, such as those resulting from
433 the presence of different call traits across calls within recordings.

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

440 Inter-call variation was limited in part by regularities in call structure, such as the presence of
441 a preceding pulse in many red-capped plover calls, the rapid frequency rise at the start of many
442 masked lapwing calls, and the generally negative association between amplitude and frequency
443 in both species. Nevertheless, substantial complexity was expressed in many calls and varied in
444 extent and nature across calls. We observed qualitative variation (at the level of different call
445 classes) across recordings of one red-capped plover chick. Limits to variation in rate of calling
446 are suggested by the uniform inter-call intervals in sequences of rapidly repeated calls (Figures
447 3A, 6B). Mechanisms of vocal control are central to acoustic variation, and vary both
448 intraspecifically and across species and higher taxa (Goller & Riede, 2013; Goller, 2021; Goller

449 et al., 2021). Mechanisms of vocalization in shorebirds are unknown, but differences within
450 species seem likely considering the great variation in modulation rates that we observed.

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

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

465

466 4.3. Call functions

467

468 The structure of distress calls of red-capped plover and masked lapwing chicks agrees with a
469 conventional picture of distress or mobbing sounds being adapted to be locatable by listeners: the
470 calls are loud and repetitive, cover a broad frequency spectrum, and often are harsh in quality
471 due to AM, FM, or nonlinear phenomena like DC (Högstedt, 1983; Davis, 1988; Brémond &

472 Aubin, 1992; Marler, 2004; Blumstein, 2007). As noted, the calls also have the quality of
473 surprisal due to their variability over multiple time scales. Assessment of these traits as
474 adaptations and understanding interspecific differences will require phylogenetic analyses and
475 experimentation to identify intended receivers, determine effects of calls and call traits on
476 receivers, and quantify the calls' active space. Behavioural observations also will be needed, and
477 many anecdotal observations exist that can guide experimentation; e.g., Simmons (1955) noted
478 that chick distress calls of little ringed plover and Kentish plover (*Ch. alexandrinus*) prompted
479 nearby siblings to scatter and attracted parents, who engaged in distraction displays. In the only
480 experiment ever conducted on a charadriid, Heckenlively (1972) observed that breeding adults
481 (parents and other birds) were attracted to playbacks of chick distress calls and produced
482 diversionary displays in response.

483 Chick distress calls of our study species shared some qualities but differed substantially in
484 structure. Both species nest on the ground and have precocial young that are not fed by the
485 parents, so both are vulnerable in similar ways to diverse native and introduced predators, but
486 both species have geographically vast and ecologically diverse ranges (Marchant & Higgins,
487 1993; del Hoyo et al., 2020; Wiersma et al., 2020). Furthermore, the study species differ in many
488 ways that must be reflected in functions and adaptations of their calls, for example in body size,
489 clutch size, patterns of parental investment, and many aspects of life history (see Material and
490 methods; Thomas, 1969; Hobbs, 1972; Lees et al., 2013; Halimubieke et al., 2020); the same will
491 undoubtedly apply also across the Charadriidae, in light of their diverse breeding ecology,
492 mating systems, and parental care (Walters, 1980, 1982, 1984, 1990; Wiersma, 1996; Eberhart-
493 Phillips, 2019; Stenzel & Page, 2019; Cerboncini et al., 2020). The study species also differ
494 greatly and vary intraspecifically in breeding density (which determines how many breeding

495 conspecific adult birds are within a call's active space), and in adult reactions to predators. For
496 example, red-capped plovers are fairly timid, though approach potential predators and engage in
497 distraction displays, whereas masked lapwings defend their nest or brood through distraction
498 displays but also through mobbing by multiple conspecific adults, and they occasionally strike
499 potential predators physically (including humans; Moffat, 1981; Cardilini et al., 2013; Lees et al.,
500 2013; P. Temple-Smith in litt., 6 August 2021). In the present state of our meager knowledge
501 (even just about intended recipients), we cannot interpret acoustic differences between the
502 species in relation to any of these factors.

503 Nonlinear phenomena are widespread in calls of vertebrates, including when animals are
504 under stress (see Introduction). Distress calls that contain nonlinear phenomena may be more
505 effective at inducing responses in conspecific or heterospecific listeners, in countering
506 habituation in listeners, or facilitating individual identification (Fitch et al., 2002; Kasirova et al.,
507 2005; Volodin et al., 2005; Volodina et al., 2006; Slaughter et al., 2013; Blesdoe et al., 2014). In
508 shorebirds, nonlinear phenomena are present in distress calls (Adret, 2012; this study), but also
509 occur in other circumstances and in other kinds of vocalizations in both chicks and adults
510 (Nethersole-Thompson & Nethersole-Thompson, 1979; Miller, 1984; Ward, 1989; Byrkjedal &
511 Thompson, 1998; Miller, 1996; Sung et al., 2005; Bergmann et al., 2008; Adret, 2012;
512 Dragonetti et al., 2013a, b; Pieplow, 2019). Unlike in distress calls of chicks, nonlinear
513 phenomena are stereotyped and occur at specific points in nuptial calls of breeding adults, such
514 as frequency jumps in *Pluvialis* species (Connors, et al. 1993; Byrkjedal & Thompson, 1998) and
515 semipalmated plover (*Ch. semipalmatus*; Sung et al., 2005), and deterministic chaos in stilt
516 sandpiper (*Calidris himantopus*; Miller, 1983). Clearly, both the form of nonlinear phenomena
517 and their predictability differ in communicative significance across such call types.

518 We recorded distress calls of red-capped plover and masked lapwing in the narrow
519 circumstance of chicks being held in the hand. Therefore, variation in call traits or classes was
520 not tied to different circumstances (vs. Green, 1975; Hicinbothom & Miller, 1999; Tallet et al.,
521 2013). It seems most parsimonious to interpret variation as reflecting the emotional state of the
522 caller, presumably to effect arousal in listeners (Bachorowski & Owren, 2003; Rendall & Owren,
523 2010; Briefer, 2020). We have avoided using the word “context” until now because it is used in
524 so many ways, and often only narrowly with reference to obvious and proximate physical or
525 social factors. In contrast, in the formulation by Smith (1977, 1997, 2009), context includes all
526 sources of information available to recipients that are outside the physical signal itself, including
527 weather, time of day, sex, or age; and social factors such as dominance rank, kinship, or
528 familiarity between sender and receiver. A pertinent example of the latter is the effect of social
529 affiliation on emotional responses to distress calls in the cockatiel (*Nymphicus hollandicus*;
530 Liévin-Bazin et al., 2018). Comparably detailed studies that address contextual factors (sensu
531 Smith) will be needed to understand functions of distress calls in charadriids.

532 **Acknowledgements**

533

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

544

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867 **Appendix**

868 **Summary of sex and body mass of red-capped plover (“plover”) and masked lapwing**
869 **(“lapwing”) chicks whose calls are shown in figures in this paper.**

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

874 Over all recordings, plover chicks averaged 9.9 g in body mass (median, 8.4; range, 2.6-
875 21.8). Six chicks weighed at the nest (i.e., 0-1 d of age) weighed 4.2 ± 1.06 (SD) g (average and
876 median were identical; range, 2.6-5.5); in their large sample of newly hatched chicks, Lees et al.
877 (2019) estimated body mass as 5.3 ± 0.06 g. Growth up to 2 weeks of age is undocumented for
878 this species, and varies greatly (range, ~13-28) after that (up to ~ 4 weeks of age; Lees et al.
879 2019).

880 Recorded lapwing chicks averaged 42.9 g in body mass (median, 29.0; range, 7.4-209).
881 Those figures correspond to chicks ranging from newly hatched to about 5-7 weeks of age
882 (average ~2 weeks; median ~1 week; Temple-Smith, 1969; Thomas, 1969; Moffat, 1981).
883 Thirteen chicks weighed at the nest averaged 20.8 ± 2.67 g in body mass (median, 21.5; range,
884 15.3-24.3), compared with 20.8 ± 0.15 in the study by Lees et al. (2019).

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

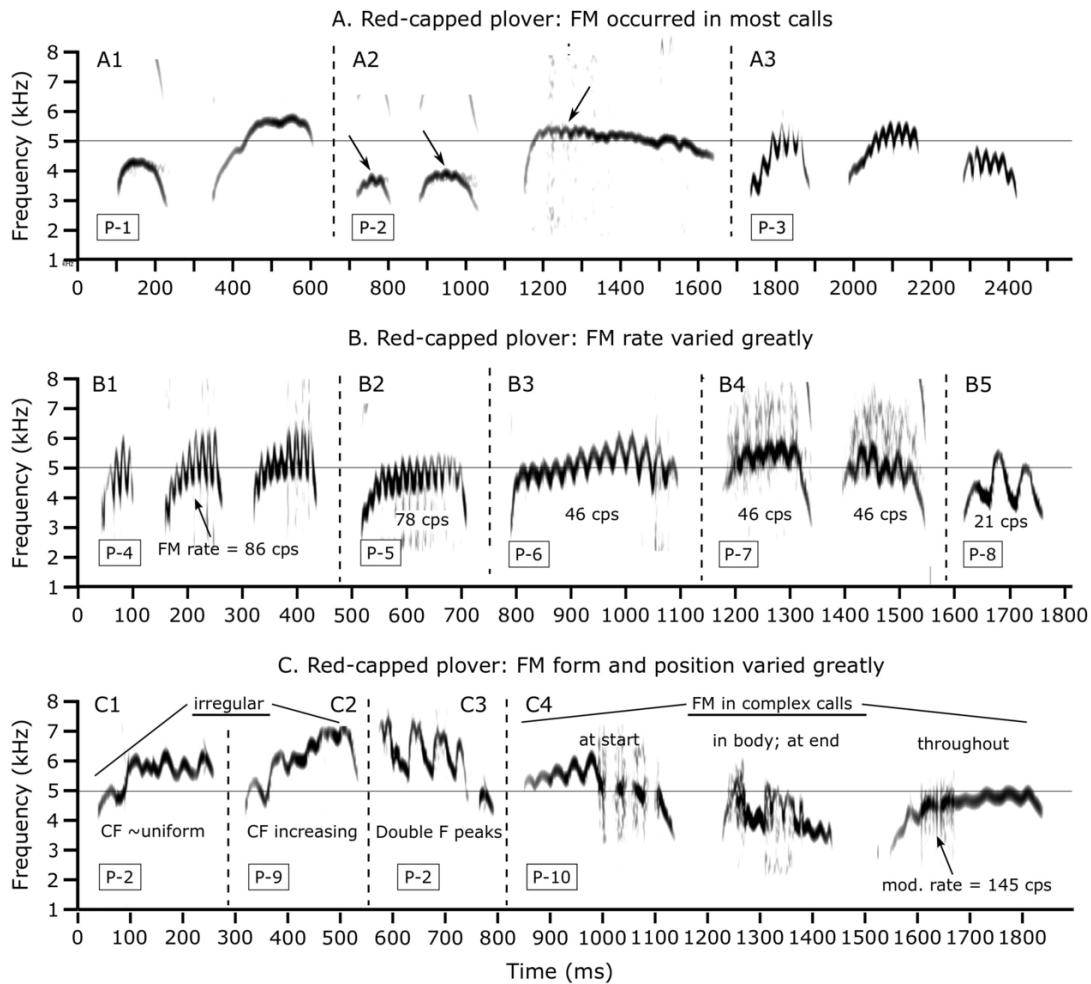
888

889 **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.
890 **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

891 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**:
892 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,
893 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;
894 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.

895 **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**:
896 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**:
897 4B2; M; unknown mass. **L-9**: 4B3; F; 44.6 g. **L-10**: 4B4, 5D4, 6A4; M; 83.0 g. **L-11**: 4B5; F;
898 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;
899 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,
900 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;
901 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;
902 133.0 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;
903 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
904 g. **L-35**: 6B; M; 36.0 g. **L-36**: 6C; M; 45.2 g. **L-37**: 6D; M; 18.5 g.

Figures

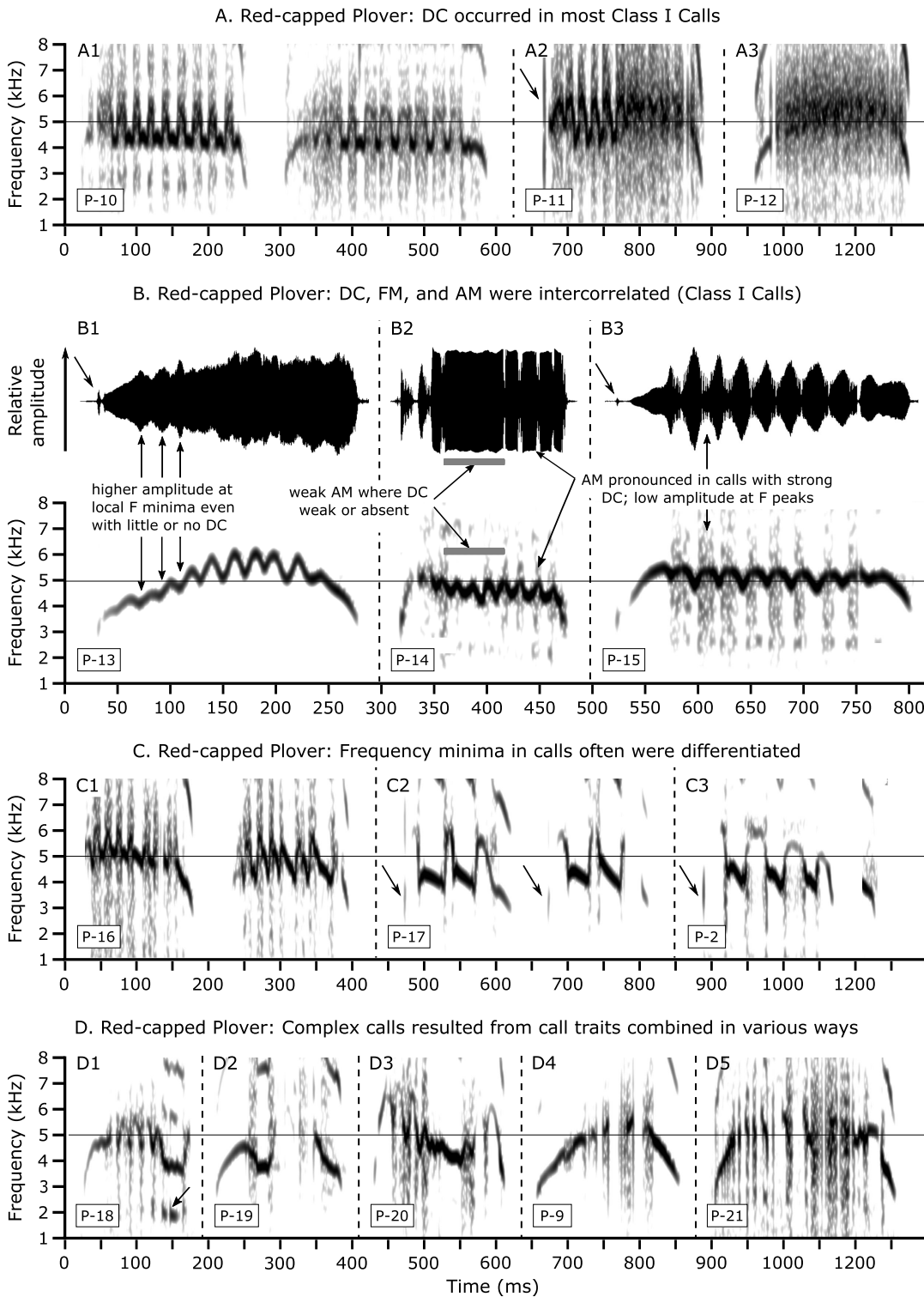


906

907 **Figure 1.** Frequency modulation (FM) in calls varied greatly within and across red-capped
 908 plover chicks. **A**, Calls varied in the frequency range they covered; small fluctuations in
 909 frequency are marked by arrows in **A2**. **B**, FM varied greatly in rate across calls. **C**, FM
 910 sometimes was irregular or complex, and varied in presence or extent in complex calls;
 911 extremely rapid FM was rare. Calls in panels **A1-A3**, **B1**, **B4**, and **C4** were not successive and
 912 the intervals shown between them are arbitrary. Plover chick numbers (P-) denote different
 913 individuals, and are consistent within and across figures. Information on body mass, sex, and
 914 age (when known) is in the Appendix. The horizontal lines at 5 kHz are visual guides.

915 Analysis settings are as stated in Methods, except for panel A, for which number of points per
916 analysis frame = 512.

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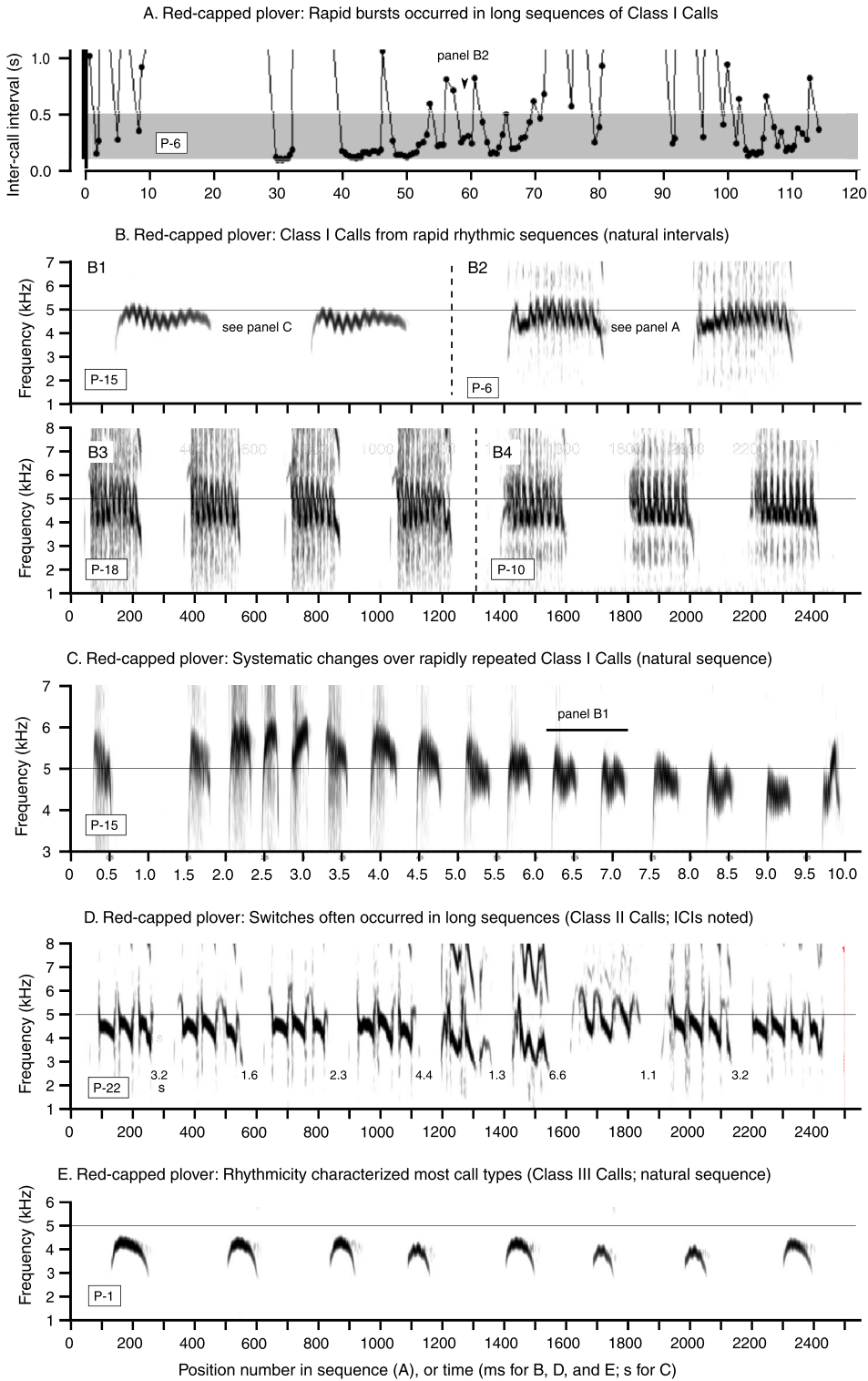
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919 **Figure 2.** *Class I Calls* of red-capped plover chicks varied in the expression and placement of

920 deterministic chaos (DC), the structure of non-DC tonal parts of calls, and frequency and

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

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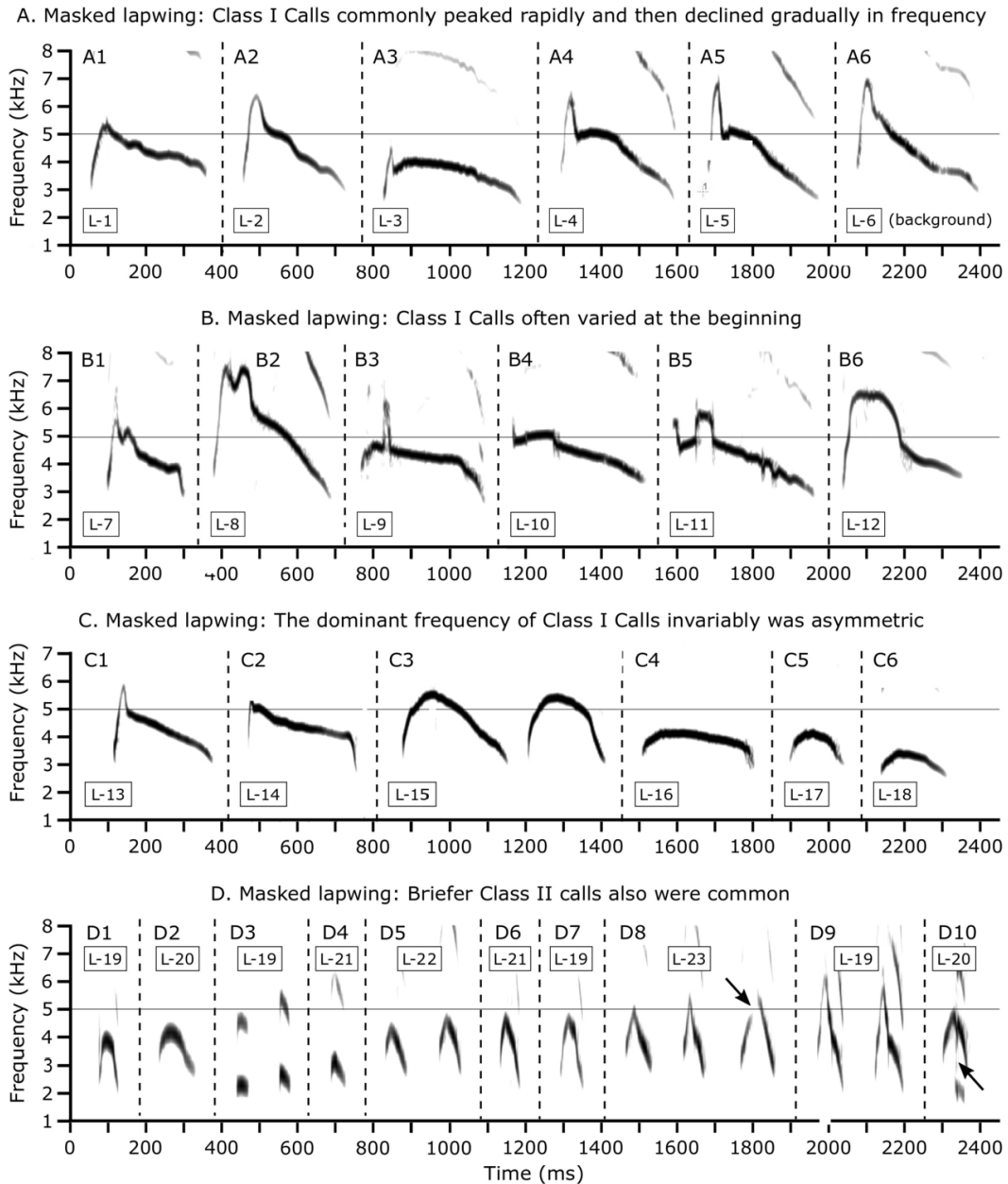
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Figure 3. The temporal pattern of call delivery by red-capped plover chicks varied within and

935

across call types. **A**, *Type I Calls* were uttered irregularly but often were given in bursts, with

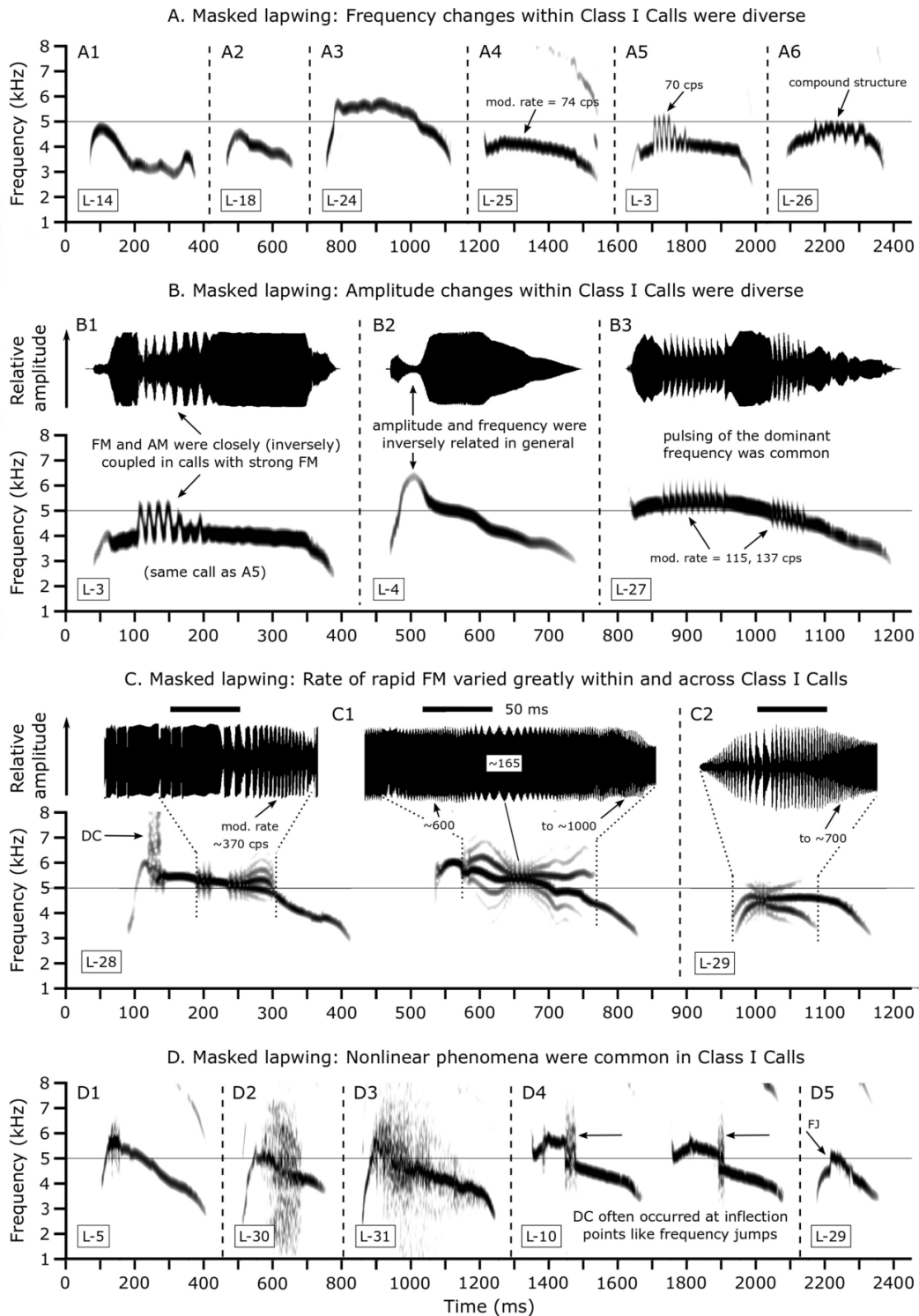
936 brief intervals between calls. **B**, Four examples of successive *Type I Calls* from bursts; natural
937 intervals are shown. **C**, Successive gradation in call characteristics occurred over bursts of
938 *Type I Calls*, despite close similarity between immediately successive calls (spectrogram
939 shown on limited frequency scale, to emphasize changes in frequency; natural intervals
940 shown). **D**, *Type II Calls* frequently were given irregularly in long sequences, though not
941 commonly in bursts. In the sequence illustrated, three other kinds of call were given before
942 *Type II Calls* resumed (intervals between successive calls noted). **E**, The uncommon tonal
943 *Type III Calls* sometimes were given in ~rhythmic sequences (part of longer sequence shown;
944 natural intervals between calls are shown). Plover chick numbers (P-) denote different
945 individuals, and are consistent within and across figures. Information on body mass, sex, and
946 age (when known) is in the Appendix. The horizontal lines at 5 kHz are visual guides.
947 Frequency scales in panels **B** and **E** were cropped to economize on space. Analysis settings
948 are as stated in Methods.
949



950

951 **Figure 4.** We recognized several broad classes of calls of masked lapwing chicks. **A**, *Type I*
 952 *Calls* were long and tonal. They often began with a sharp rise in frequency, followed by a
 953 slower decline. **B**, The start of *Type I Calls* was variable. **C**, *Type I Calls* often began with
 954 little or no frequency rise, but the trajectory of dominant frequency was almost always
 955 asymmetric in frequency. **D**, *Type II Calls* were brief vocalizations. The arrows point to a
 956 frequency gap due to low amplitude (**D8**) and deterministic chaos (**D10**). Calls in **C3**, **D3**, **D5**,

957 **D8**, and **D9** were not successive and the intervals shown between them are arbitrary. Lapwing
958 chick numbers (L-) denote different individuals, and are consistent within and across figures.
959 Information on body mass, sex, and age (when known) is in the Appendix. The horizontal
960 lines at 5 kHz are visual guides. Analysis settings are as stated in Methods, except number of
961 points per analysis frame = 512 for panels **A**, **B**, and **C**, and 256 for panel **D**.
962



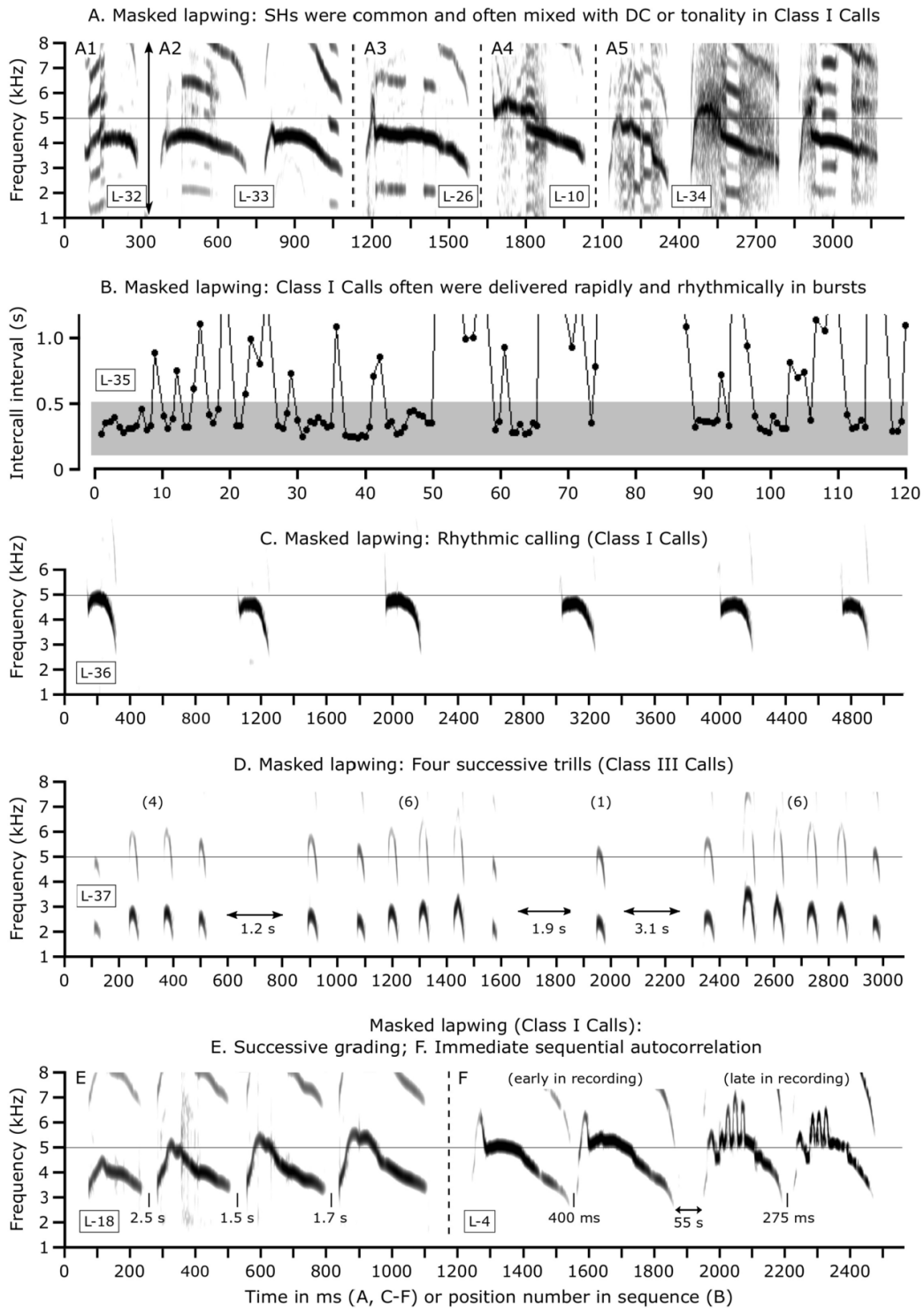
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964 **Figure 5.** Changes in frequency and amplitude, and nonlinear phenomena, were diverse in calls

965 of masked lapwing chicks. A, Slow frequency modulation (FM) occurred in parts or all of

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

977



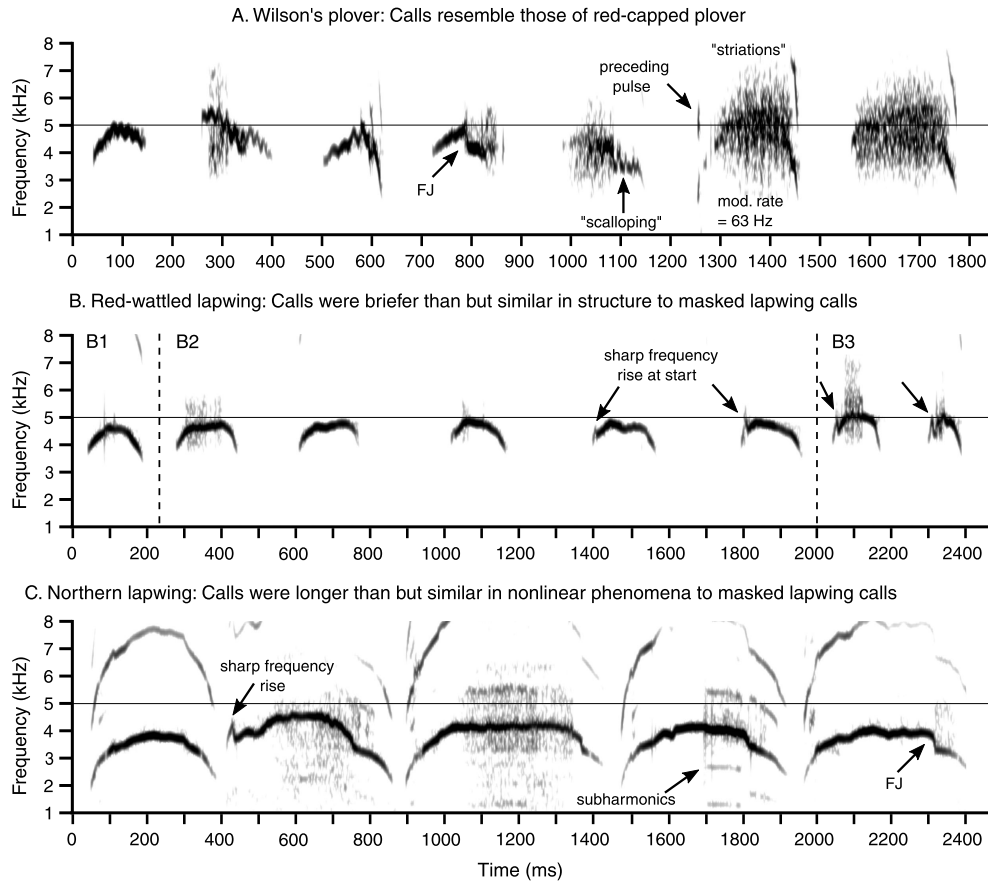
978

979 **Figure 6.** A, Subharmonics (SHs) were common in *Class I Calls* of masked lapwing. B, *Class I*

980 *Calls* were uttered irregularly but often were given in bursts, with brief intervals between

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

991



992

993 **Figure 7.** Distress calls of other plover and lapwing species. **A**, Wilson's plover calls resembled

994 those of red-capped plover in some key features (see text; note frequency jump, FJ). **B**, Red-

995 wattled lapwing: single call (**B1**), first five calls in 7-part series (**B2**); and second and third

996 calls in other 7-part series (**B3**); natural intervals between calls are shown for **B2** and **B3**. Note

997 deterministic chaos and the sharp rise at the beginning of calls (arrows), as in Masked

998 Lapwing. **C**, Northern lapwing: five calls (not in sequence). Note deterministic chaos,

999 subharmonics, and FJ with associated deterministic chaos (latter two marked by arrows). Calls

1000 in **A** and **C** were not successive and the intervals shown between them are arbitrary. Sources

1001 of sounds are provided in Methods. The horizontal lines at 5 kHz are visual guides. Analysis

1002 settings are as stated in Methods, except number of points per analysis frame = 512 for panels

1003 **C** and **D**.