


Short Communication

Vocal traits of shorebird chicks are related to body mass and sex

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Acoustic communication is critical during early life phases in precocial birds; for example, adult alarm calls can elicit antipredator behaviour in young, and chick vocalizations can communicate information to parents about chick identity, condition, location, sex or age. We opportunistically recorded Red-capped Plover *Charadrius ruficapillus* and Southern Masked Lapwing *Vanellus miles novaehollandiae* distress calls of chicks while they were in the hand and analysed the calls to determine whether call structure is related to sex or body mass (a proxy for age). Our study provides the first evidence for charadriid chicks of (1) a sexual difference in call structure and rate and (2) gradual growth-related changes in call structure and rate, across chicks. We provide a foundation for further studies of shorebird vocalizations during growth, which may elucidate the development and functional significance of such vocalizations.

Keywords: body growth, *Charadrius ruficapillus*, distress call, sexual difference, *Vanellus miles novaehollandiae*, vocal development.

Acoustic communication can be critical in the early life of birds. In nestlings, begging calls can solicit parental feeding, contact calls can help parents locate and identify offspring, and distress calls given during social separation, environmental challenges or handling can startle predators or elicit help from parents, conspecifics, or

other nearby species (Stefanski & Falls 1972, Sethi *et al.* 2012). Several studies have investigated the function of calls in juvenile birds (e.g. Desmedt *et al.* 2020) but few have considered the structure or development of juvenile calls. Developmental changes in chick vocalizations can allow parents to assess chick condition (e.g. Goedert *et al.* 2014) and have been documented for some precocial species (e.g. Würdinger 1970, Desmedt *et al.* 2020). With some exceptions (Herting *et al.* 2001, Odom & Mennill 2010), there is a general trend for the dominant frequency of calls to be inversely related to body mass or size across species, possibly due to the greater mass of vocal structures or respiratory muscles (Suthers & Zollinger 2004). Larger birds also may be constrained in producing higher frequencies, for example via stronger constraints on tissue elasticity with larger anatomical structures (Demery *et al.* 2021). Intra-specifically, changes in vocalizations can occur gradually as body mass increases with age (Dragonetti *et al.* 2013), or in a step-like fashion (Klenova *et al.* 2014).

Vocal traits can also differ between sexes, and play important roles in reproduction, territorial defence and other social activities (Buck *et al.* 2021). Sexual differences emerge at various times during development in different species, from several days old to after fledging (Cosens 1981, Saino *et al.* 2008) to as late as at sexual maturity (Klenova *et al.* 2014), but no general patterns are evident (Tikhonov 1986, ten Thoren & Bergmann 1987a,b, Volodin *et al.* 2015). The nature of sexual differences in calls also varies across species, for example in the dominant frequency (ten Thoren & Bergmann 1987a), duration (Tikhonov 1986) or amplitude (Saino *et al.* 2008) of calls. Some interspecific variation in the occurrence and nature of sex-related differences may result from patterns of growth, sexual differences in body size, or ecological or social factors (Saino *et al.* 2003, Volodin *et al.* 2015, Austin *et al.* 2021).

Vocal communication in shorebirds can help keep precocial young close to their parents and away from predators, and might also play a role in mediating sexual differences in the survival, parental care and dispersal of young (Pakanen *et al.* 2015, Eberhart-Phillips *et al.* 2017, Lees *et al.* 2018, 2019). However, despite a plethora of studies and reviews on social organization, breeding biology, behavioural ecology and communication in shorebirds, vocal development has been examined in only two species. Adret (2012) quantified age-related changes in measures of call frequency and noted a sexual difference in call rates for Pied Avocet *Recurvirostra avosetta* chicks. Dragonetti *et al.* (2013) described qualitative changes of Eurasian Stone-curlew *Burhinus oedipnemus* chick calls with age. To extend knowledge of vocal communication and development in shorebirds, we investigated potential relationships of call traits to body mass and sex in chicks of two shorebird species. When in the hand for banding and blood sampling,

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chicks of Red-capped Plover *Charadrius ruficapillus* and Southern Masked Lapwing *Vanellus miles novaehollandiae* ('Plover' and 'Lapwing' hereafter) often utter distress calls. We recorded these calls to document their structure (Miller *et al.* 2022), and to determine whether they change with body mass (a proxy for age) or differ between sexes. We predicted that call structure, especially frequency-related characteristics, would change with increasing body mass (Demery *et al.* 2021). In some precocial bird species, it would probably be beneficial for parents to distinguish the sex of their offspring, for purposes of parental defence and care (Barrios-Miller & Siefferman 2013, Lees *et al.* 2018). We therefore predicted sexual differences in chick calls. Our study provides the first account of call development for any species of Charadriidae.

METHODS

We studied Plovers from October 2017 to March 2018 (Cheetham Wetlands, Victoria, Australia; 37°54'S, 144°47'E; 420 ha). Male chicks have slightly longer tarsi than females (Lees *et al.* 2019), but otherwise the sexes are indistinguishable until their second immature plumage (Marchant & Higgins 1993). We studied Lapwings, which have sexually indistinguishable young (Lees *et al.* 2018), from June to September 2018 (Phillip Island, Victoria, Australia; 38°29'S, 145°14'E; 10 000 ha). Parents brood and defend their chicks, which attain the capacity for sustained flight at approximately 35 days (Plovers) and 45 days (Lapwings) (Temple-Smith 1969, Marchant & Higgins 1993, Lees *et al.* 2018).

We conducted extensive searches for nests from vehicles and on foot. Upon discovering a nest, we estimated approximate hatching dates by floating the eggs (Liebezeit *et al.* 2007), assuming incubation periods of 30 days (Plovers) and 32 days (Lapwings) (Marchant & Higgins 1993, Lees *et al.* 2018). We returned to nests around our estimated hatching dates to capture chicks. Occasionally, we captured older unbanded chicks away from known nests. For each captured chick, we measured body mass (Pesola spring balance: ± 0.1 g), and tarsus, tarsus plus toe, culmen and head plus culmen lengths (dial calliper: ± 0.1 mm; Rogers *et al.* 1990). All body measurements are provided within the Supporting Information (Tables S1 and S2). We use only body mass as a proxy for age because: (1) we did not know the exact ages of most chicks, (2) all variables describing body size were highly inter-correlated ($r_{\text{Pearson}} \geq 0.75$ for all pairwise combinations) and (3) a relationship of call structure to body mass occurs in other species (Martin *et al.* 2011). We also obtained *c.* 50 μL of blood from the tarsal vein of each chick, which permitted genetic sexing (DNA Solutions™, Wantirna, Victoria, Australia). We

recaptured and measured (excluding blood extraction) five Plover chicks (mean interval between captures: 8.6 ± 3.4 days, range 6–14 days, $n = 5$) but did not recapture any Lapwing chicks. Chick and brood identity were determined by the use of individually numbered metal leg bands and the location of chicks upon first sighting/capture (within the nest or close proximity to marked siblings and/or identifiable parents). We cite mean \pm sd throughout.

Call recording and acoustic analysis

We processed chicks singly (Plover: 9.8 ± 5.1 min, $n = 26$; Lapwing: 5.7 ± 2.9 min, $n = 95$) in a quiet, sheltered location. We recorded their vocalizations using a portable digital recorder (Roland R-26, WAVE format, 44.1 kHz sampling rate, and 16-bit depth) and an omnidirectional Sennheiser ME 2-II microphone (50–18 000 Hz frequency response) held approximately 5 cm from the chick. Recordings usually included multiple calls of the chick being handled, and sometimes included calls of siblings held nearby, but these calls were distinguishable in our recordings; we assume they do not influence the variables we measure. For the five Plover chicks that were recaptured, we analysed vocalizations from their second capture. The number of calls per recording of each individual chick varied (Plover: 92.9 ± 74.9 calls, range 1–248 calls, $n = 26$ chicks; Lapwing: 65.7 ± 70.4 calls, range 1–336 calls, $n = 95$ chicks).

We provide a detailed account of acoustic analysis in the Supporting Information (Appendix S1). Briefly, after filtering calls, we identified start and end times of each call and we divided each call into a series of contiguous 2.9-ms time bins. We measured the Shannon spectral entropy and dominant frequency from a mean power spectrum for each bin. We used six call traits for analyses: (1) call duration, the time interval between the start and end of a call (seconds); (2) inter-call interval (ICI), the interval between the end of a call and the start of the next (seconds); (3) entropy, the average of all spectral entropy values within a call (unitless); (4) minimum dominant frequency (kHz); (5) dominant frequency range, the difference between a call's minimum and maximum dominant frequency (kHz); and (6) frequency modulation. For Lapwings, we calculated frequency modulation by fitting a series of polynomial regressions (up to 12th order) to the dominant frequency and time values of the call, selecting the best-fitting model (Supporting Information Fig. S1). For each 2.9-ms time bin, we calculated the slope of the tangent to the polynomial curve and used the range of slopes across the call as our measure of frequency modulation (kHz/s; Supporting Information Fig. S1). For Plovers, polynomial regression curves could not adequately model the frequency

modulations. Instead, we defined frequency modulation as the cumulative absolute change in dominant frequency across all 2.9-ms time bins, divided by call duration (kHz/s). See Supporting Information Fig. S3 for call variation between Plovers and Lapwings, particularly in the presence and extent of frequency modulation. We also calculated maximum dominant frequency as a separate variable, but excluded it because it was highly correlated with dominant frequency range for both species ($r_{\text{Pearson}} = 0.86$ and $r_{\text{Pearson}} = 0.89$ for Plovers and Lapwings, respectively) and because statistical models exhibited poor fit (see below). Correlations among the remaining six variables were all < 0.7 . Not all variables could be calculated from every call.

Statistical analysis

Separate generalized linear mixed models examined possible relationships among call traits, body mass and sex for each species (one model per call trait and species). We included body mass and sex as main effects in all models. For some traits, an interactive effect between body mass and sex might occur, although we had no *a priori* reason to expect this. Nevertheless, for each analysis, we compared a model with main effects only with a model with main effects plus an interaction term between body mass and sex. We included chick identity nested within brood identity as a random effect to account for possible dependencies among calls recorded from the same chick or brood. We specified a Toeplitz covariance structure (Glaz & Yeater 2020) to account for sequential autocorrelation between calls. We based model selection on the Akaike Information Criterion (AIC) values, with best models being identified where they differed from the alternative candidate model by $\Delta\text{AIC} > 2$ (Symonds & Moussalli 2011). Where candidate models appeared to be equally informative ($\Delta\text{AIC} \leq 2$), we did not include the interaction term in the final model (the main-effects-only model always had the lowest AIC).

We tested model assumptions and evaluated model fit by comparing observed data with simulated data derived from the model (Hartig 2018). For Lapwings, many calls had a measured frequency modulation of zero, which resulted in poor model fit (i.e. outliers had significant leverage) that could not be improved through the use of zero-inflated models (Brooks *et al.* 2017). We retained the zeros within the final model because they were not errors, and their removal did not change the results with respect to statistical significance (Supporting Information, Fig. S2 and Table S3). When analysing entropy, we excluded calls for which the recording was saturated (the input of a signal was greater than the output, creating clipping and distortion to the shape of the waveforms; Plover, 39.7% of calls excluded, $n = 939$ of

2365 calls; Lapwing, 53.7% of calls excluded, $n = 3588$ of 6683 calls). Saturation can affect entropy, and the entropy differed significantly between saturated and non-saturated calls (Supporting Information, Table S4). When analysing ICIs, we excluded chicks with fewer than 10 calls recorded (Plover, $n = 3$; Lapwing, $n = 20$) because calling was too sporadic to get a reliable measure of ICI. We used the median ICI of each individual's recording (excluding any sibling calls), because we had no objective way of distinguishing calling bouts.

Transformations of data were performed to improve distribution and model fit. We applied a reciprocal transformation on body mass for both species for all models. For Lapwings, we added a constant (i.e. 2) and then logarithmically transformed the data for frequency modulation, dominant frequency range and ICI. We performed the same transformation for dominant frequency range and ICI for Plovers; however, as entropy was left-skewed, we subtracted values from a constant (2) and then log-transformed the data. We indicate probability distributions and link functions within the tables.

We performed analyses in R using the packages *glmmTMB* for running mixed models, *DHARMA* for model assumption testing, *bbmle* for calculating ΔAIC values, *psych* for creating histograms and scatterplots, base R for creating and observing simulated data, and *ggplot2* and *ggeffects* for figures (Wickham 2016, Brooks *et al.* 2017, Hartig 2018, Lüdecke 2018, Bolker & R Core Team 2020, Revelle 2021). We controlled the experiment-wise type I error rate by applying a Bonferroni correction, which adjusted our α value from 0.05 to 0.0083. For figures, ICIs, entropy and dominant frequency range were back-transformed and presented on the original scale in figures. Estimated marginal means (hatched and solid lines) and 95% confidence intervals (grey shading) were calculated using *ggeffects* (Lüdecke 2018).

RESULTS

For Plovers, we recorded 2600 vocalizations from 26 individual chicks (1–248 calls per chick; 570 calls from nine females and 2030 calls from 17 males), over the body mass range of 3.5–20.5 g (mean \pm sd: 8.5 ± 4.6 g). This range corresponds to chick ages from the day of hatching to approximately 4 weeks of age (Lees *et al.* 2019).

For Lapwings, we recorded 6835 vocalizations from 95 individual chicks (1–336 calls per chick; 3174 calls from 46 females and 3661 calls from 49 males), over the body mass range of 15.2–177.0 g (43.6 ± 30.2 g). This range corresponds to chick ages from the day of hatching to approximately 5 weeks of age (Thomas 1969, Moffat 1981).

For Plovers, ICIs were shorter for males than for females and, as mass increased, ICIs and the dominant

Table 1. Results of separate generalized linear mixed models investigating possible relationships between body mass (reciprocal transformation) and sex (the interaction was selected for inclusion for the frequency range model only) with call duration, inter-call interval (ICI), entropy, minimum frequency, frequency range and frequency modulation for Red-capped Plovers and Masked Lapwings. Chick identity nested within brood identity was included as a random effect for all analyses. We specified a Toeplitz covariance structure for all models. The reference category for sex was female. Estimates are presented as estimates of coefficients \pm se for fixed effects, and variance \pm sd for the random effect of identification nested within brood identity. The probability distribution was Gaussian and we used an identity link function for all variables except frequency modulation (Plovers), for which we used a negative binomial (linear parameterization) distribution with a log link.

Species	Response variable	Model terms	Estimates	z	P
Red-capped Plover	Call duration $n = 2365$ calls	Body mass ^b	0.181 \pm 0.126	1.437	0.151
		Sex	0.028 \pm 0.019	1.476	0.140
		Chick ID: brood ID	0.002 \pm 0.044	NA	NA
	ICI ^a $n = 23$ chicks	Body mass ^b	3.446 \pm 0.956	3.603	< 0.001
		Sex	-0.419 \pm 0.153	-2.737	0.006
		Chick ID: brood ID	0.008 \pm 0.089	NA	NA
	Entropy ^a $n = 1426$ calls	Body mass ^b	-0.049 \pm 0.054	-0.895	0.371
		Sex	0.003 \pm 0.008	0.371	0.711
		Chick ID: brood ID	0.000 \pm 0.019	NA	NA
	Minimum dominant frequency $n = 2365$ calls	Body mass ^b	-0.275 \pm 0.529	-0.520	0.603
		Sex	-0.008 \pm 0.081	-0.093	0.926
		Chick ID: brood ID	0.030 \pm 0.173	NA	NA
	Dominant frequency range ^a $n = 2365$ calls	Body mass ^b	5.723 \pm 1.679	3.408	< 0.001
		Sex	0.602 \pm 0.406	1.484	0.138
		Body mass*Sex	-3.574 \pm 2.153	-1.660	0.100
Chick ID: brood ID		0.126 \pm 0.357	NA	NA	
Frequency modulation $n = 2365$ calls		Body mass ^b	1.664 \pm 0.703	2.368	0.018
Masked Lapwing	Call duration $n = 6683$ calls	Sex	-0.100 \pm 0.108	-0.930	0.352
		Chick ID: brood ID	0.057 \pm 0.239	NA	NA
		Body mass ^b	-0.299 \pm 0.475	-0.631	0.528
	ICI ^a $n = 76$ chicks	Sex	0.014 \pm 0.013	1.024	0.306
		Chick ID: brood ID	0.005 \pm 0.071	NA	NA
		Body mass ^b	1.980 \pm 2.679	0.739	0.460
	Entropy $n = 3096$ calls	Sex	0.011 \pm 0.084	0.134	0.893
		Chick ID: brood ID	0.014 \pm 0.117	NA	NA
		Body mass ^b	2.283 \pm 0.476	4.795	< 0.001
	Minimum dominant frequency $n = 6683$ calls	Sex	-0.018 \pm 0.015	-1.270	0.204
		Chick ID: brood ID	0.004 \pm 0.061	NA	NA
		Body mass ^b	-3.269 \pm 1.688	-1.940	0.053
	Dominant frequency range ^a $n = 6683$ calls	Sex	-0.010 \pm 0.051	-0.190	0.850
		Chick ID: brood ID	0.061 \pm 0.248	NA	NA
		Body mass ^b	0.548 \pm 0.556	0.986	0.324
Sex		-0.069 \pm 0.030	-2.361	0.018	
Body mass*Sex		2.210 \pm 0.726	3.043	0.002	
Frequency modulation ^a $n = 6619$ calls	Chick ID: brood ID	0.004 \pm 0.065	NA	NA	
	Body mass ^b	6.145 \pm 0.951	6.46	< 0.001	
	Sex	-0.084 \pm 0.030	-2.810	0.005	
	Chick ID: brood ID	0.016 \pm 0.126	NA	NA	

^aLogarithmically transformed data. ^bTo aid interpretation, note that the reciprocal transformation reflects the sign of coefficients.

frequency range of calls decreased (Table 1, Fig. 1). There were no significant relationships of call duration, entropy, minimum dominant frequency, or frequency modulation to sex or body mass.

For Lapwings, frequency modulation was lower for males than for females (Table 1; Fig. 2). For both sexes, dominant frequency range decreased with increasing

body mass; however, the decline was greater in males, resulting in a lower dominant frequency range than for females (Table 1; Fig. 2). As body mass increased, frequency modulation and entropy of Lapwing calls decreased (Table 1; Fig. 2). Call duration, minimum dominant frequency and ICI were not predicted by sex or body mass.

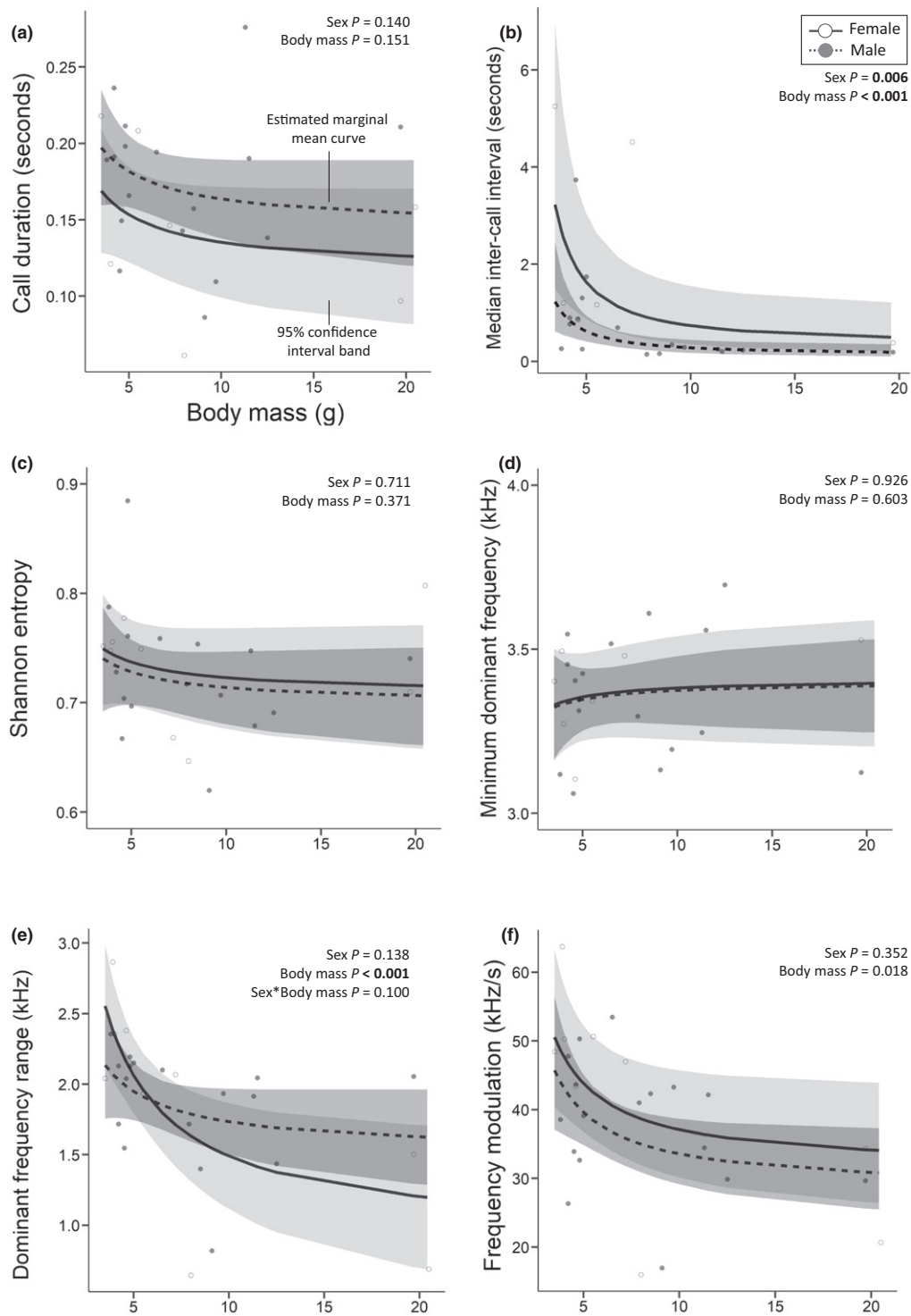


Figure 1. For Red-capped Plovers, call duration did not vary with body mass or sex (a), but inter-call intervals (ICIs) decreased with increasing body mass and were shorter in males (b). Entropy and minimum dominant frequency did not vary with body mass or sex (c,d). Dominant frequency range decreased with increasing body mass (e), but frequency modulation did not vary with body mass or sex (f). Estimated marginal means (hatched and solid lines) and 95% confidence intervals (grey shading) are shown.

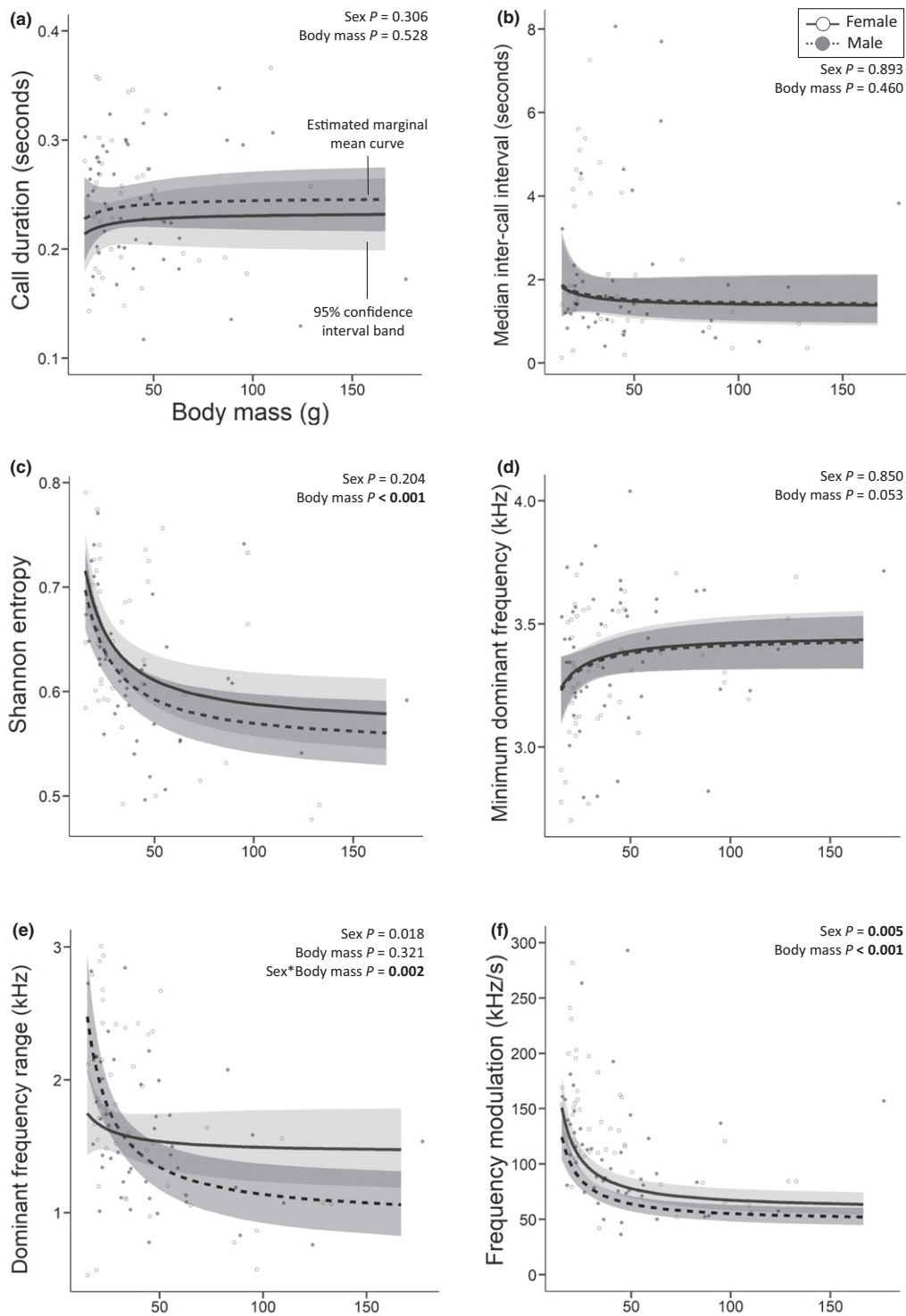


Figure 2. For Masked Lapwings, call duration and inter-call intervals (ICIs) did not vary with body mass or sex (a,b), but entropy decreased with increasing body mass (c). Minimum dominant frequency did not vary with body mass or sex (d), but dominant frequency range decreased with body mass and the decline was greater in males (e). Frequency modulation decreased with body mass and was lower in males (f). Estimated marginal means (hatched and solid lines) and 95% confidence intervals (grey shading) are shown.

DISCUSSION

Multiple call traits were associated with body mass; vocal traits changed gradually, as has been described previously in growing shorebirds (Adret 2012, Dragonetti *et al.* 2013), although repeated measurements of the same individuals are required to confirm this. For both study species, minimum dominant frequency was not associated with body mass, whereas dominant frequency range decreased with increasing body mass, consistent with maximum dominant frequency declining during growth in birds (Würdinger 1970, Adret 2012, Dragonetti *et al.* 2013). The decline in frequency modulation with increasing body mass in Lapwings (and a similar but non-significant pattern for Plovers) is consistent with the idea that frequency fluctuations within a call decrease with increasing body mass. Large bill size may impede the ability to quickly open and close the bill, therefore limiting the rate of frequency modulation (Podos 2001, Demery *et al.* 2021), though other explanations may exist, such as changes to the vocal tract with growth. Shorter ICIs were associated with heavier body masses in Plovers, which might reflect the capacity of older, heavier chicks to control airflow through vocal structures (Franz & Goller 2002, Zvonov 2011). We did not detect a change in call duration with age in either species (but see Adret 2012). Heavier Lapwing chicks produced calls that were more tonal (i.e. reduced entropy), possibly associated with increased motor control of the upper vocal tract (Podos *et al.* 1995). As chicks age, variation in call structure may reflect attempts to utter adult-like calls, as described for other shorebirds (Adret 2012, Dragonetti *et al.* 2013).

For Lapwings, frequency modulation was higher in females and, for Plovers, male chicks had higher call rates than females. Compared with females, male Red-capped Plover chicks had shorter ICIs from hatching; cooing rates were also higher in male Pied Avocet chicks until the age of 9 months (Adret 2012). A faster repetition rate of distress calling might increase response intensity by adult defenders (Wheatcroft 2015), which could contribute to the higher survival of male over female chicks reported for several plover species (Sandercock *et al.* 2005, Pakanen *et al.* 2015, Saunders & Cuthbert 2015, Eberhart-Phillips *et al.* 2017; but see Lees *et al.* 2019). For Lapwings, dominant frequency range declined with body mass more in males than in females, resulting in the development of a lower overall dominant frequency range in males. Frequency modulation was also lower in males than in females from hatching and throughout growth, suggesting differences in calls between the sexes at hatching. The sexes may differ in the size or rate of development in vocal anatomy, or the vocal control of these structures (Ballintijn & ten Cate 1997a,b, Gahr 2007, Volodin *et al.* 2015).

Overall, calls between the sexes were similar in most respects. Contextually, this study analysed distress calls

(loud, harsh and locatable; Sethi *et al.* 2012), which are probably under the influence of natural selection (Martin *et al.* 2011). Some non-distress vocalizations (e.g. contact calls) might communicate the caller's sex, whereas distress calls may not (Austin *et al.* 2021). Even when a sex is 'preferred' by parents, calls of the non-preferred sex are expected to evolve to be similar to those of the preferred sex (Austin *et al.* 2021). Furthermore, distress calls emitted by chicks may serve to communicate with siblings, other conspecifics, the predator or some combination of these. Future studies should therefore investigate associations between shorebird chick calls and sex using the full repertoire of chick calls, and across species whose adult call repertoires and characteristics vary between sexes. We note our limited sample size, bias toward young chicks and imbalance in sex ratio for Plovers (34.6% were female), and suggest further study would be desirable. We also note that we did not repeatedly measure the same individuals, so cannot unambiguously exclude effects such as those associated with survival bias.

This research complies with the current laws of Australia and was conducted in accordance with protocols reviewed and approved by the Deakin University Animal Ethics Committee (Permit numbers B01 2018, B11 2017 and B12 2017) and the Department of Environment, Land, Water and Planning (Permits 10008437 and 10008619). The authors minimized impacts on chicks by only collecting data on days of suitable weather (e.g. no rain or extreme heat) and by generally avoiding recaptures. This project was supported by The Holsworth Wildlife Research Endowment and The Ecological Society of Australia. M.A.W. was supported during write-up by the Beach Ecology and Conservation Hub (BEACH, Venus Bay). Thanks to Dr Peter Dann (Phillip Island Nature Parks) and Rangers at the Point Cook Coastal Park (Ron Cuthbert, Russell Brooks, Mark Cullen and Bernie McCarrick) for their assistance, to Ekaterina Ershova for her help in translating Russian material and to Rachel Adams (Utas) for bibliographic help. Phil Battley and Ruedi Nager greatly assisted the revision of the manuscript.

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AUTHOR CONTRIBUTIONS

Kristal Nicole Kostoglou: Conceptualization (lead); Data curation (lead); Formal analysis (equal); Funding acquisition (lead); Investigation (lead); Methodology (lead); Project administration (lead); Writing – original draft (lead); Writing – review & editing (lead). **Edward H. Miller:** Data curation (supporting); Formal analysis (supporting); Methodology (supporting); Writing – review &

editing (supporting). **Michael A Weston**: Conceptualization (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Supervision (lead); Writing – original draft (supporting); Writing – review & editing (supporting). **David R. Wilson**: Data curation (supporting); Formal analysis (equal); Methodology (supporting); Writing – review & editing (supporting).

ETHICAL NOTE

None.

Data Availability Statement

The datasets generated during and/or analysed during the current study are available in the figshare repository via: 10.6084/m9.figshare.14813379.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Figure demonstrating methods for calculating frequency modulation for Masked Lapwing.

Figure S2. Histogram showing the frequency distribution of log-transformed frequency modulation for Masked Lapwing chick calls.

Figure S3. Spectrogram displaying distress calls of five different Red-capped Plover and Masked Lapwing chicks.

Appendix S1. Details of the quantification of acoustic variables.

Table S1. Body measurements for all Red-capped Plover chicks.

Table S2. Body measurements for all Masked Lapwing chicks.

Table S3. Results of the generalized linear mixed model investigating the relationship between frequency modulation of Lapwing calls with outliers removed and body mass and sex.

Table S4. Results of the generalized linear mixed model investigating the relationship of body mass, sex and call saturation on call entropy for both species.

1 **SUPPORTING INFORMATION**

2 **Appendix S1** Using Raven Pro 1.6.1 (www.birds.cornell.edu/raven), we viewed each
3 recording as a waveform and spectrogram (plover, fast Fourier transform (FFT) size =
4 512 samples; lapwing, FFT size = 1024 samples; hamming window and 87.5% overlap
5 for both species). Frequency modulation was rapid in many plover calls, so we specified
6 a shorter FFT window for that species to resolve frequency changes better; this was not
7 necessary for lapwing calls, which featured little frequency modulation (Fig. S3;
8 definition below). Using spectrograms as guides, we manually marked the approximate
9 beginning and end of every call of each chick (or its identifiable sibling) on the
10 waveform. Using these time records, we then opened each call in R (R Core Team
11 2021), plus 30 ms before and after the call, using the seewave and tuneR packages
12 (Sueur et al. 2008, Ligges et al. 2018). We applied a 1000 Hz high-pass filter, which
13 reduced low-frequency background noise without affecting call structure, and
14 normalised calls to 0 dB. For lapwing calls, we adjusted the start and end times using a
15 more objective approach based on an amplitude threshold, which defined the start of
16 calls as the point where amplitude exceeded 15% of the maximum amplitude for 2 ms
17 and the end of calls as the point where amplitude fell below 15% for 2 ms. We plotted
18 the new start and end times on waveforms and spectrograms (settings as above) to
19 ensure that values derived from the amplitude threshold approach were not based on
20 artifacts. In a few cases (40 of 6835 calls), high background noise masked the start and
21 end times, so we relied on our original (manually determined) times for those calls. For

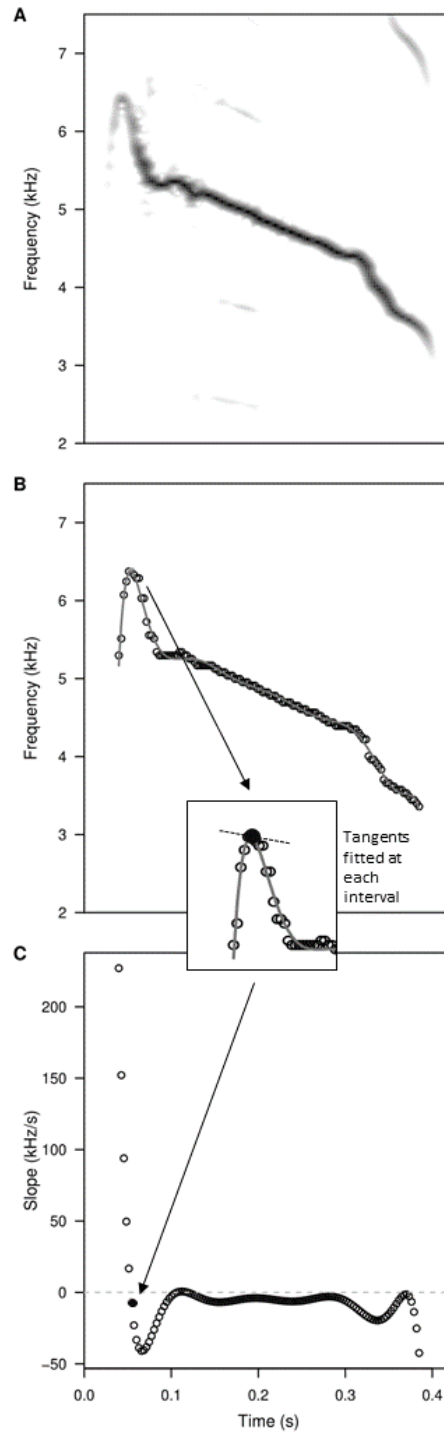
22 plover calls, low signal-to-noise ratios precluded the use of the amplitude threshold
23 approach in many calls, so we used the manually selected start and end times.

24 We divided each call into a series of contiguous 2.9-ms time bins, and, for each bin,
25 measured the Shannon spectral entropy and dominant frequency from a mean power
26 spectrum (settings as per the corresponding spectrogram listed above). Entropy is a
27 measure of tonal purity that approaches 0 for pure tones and 1 for white noise, and
28 dominant frequency is the frequency of maximum amplitude, excluding harmonics and
29 background noises. We validated our measures of dominant frequency by plotting them
30 against time and comparing the resulting plot to the corresponding spectrogram (Fig.
31 S1). In some cases, measures of dominant frequency, particularly at the start or end of
32 the call, were based on background noise rather than the call itself. If these
33 measurement errors were limited to one or two time bins (i.e. 2.9 or 5.8 ms), we
34 excluded those bins from subsequent analyses; if they occurred in more than two time
35 bins, or in the middle of the call, we excluded the entire call from subsequent analyses
36 (we thereby excluded 235 of 2600 plover calls, and 153 of 6835 lapwing calls).

37 **References**

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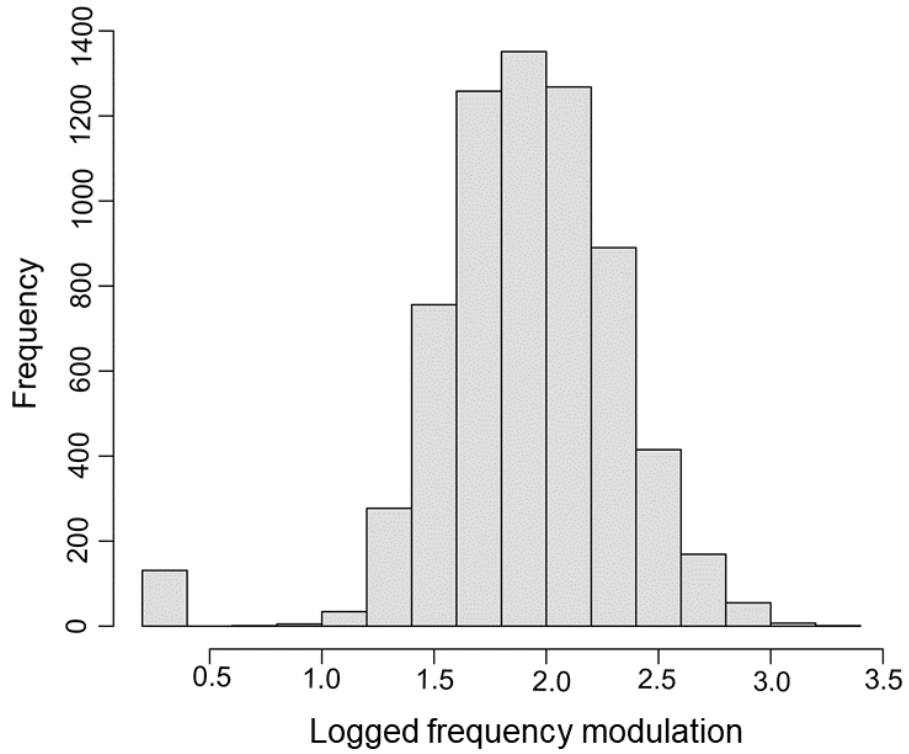


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46 Figure S1. To quantify the structure of Masked Lapwing calls we first inspected the
47 spectrogram of each call (A). Calls were then divided into contiguous 2.9-ms time bins,
48 and a mean power spectrum calculated for each bin. We measured the dominant
49 frequency of each bin from the corresponding mean spectrum and plotted it as a
50 function of time (B; open circles). We regressed dominant frequency values on time
51 using a series of polynomial regressions (first to twelfth order), and superimposed the
52 best-fitting regression on the dominant frequency values (solid line; B). We calculated
53 the slope of the tangent to the selected polynomial for every 2.9-ms interval and plotted
54 it as a function of time (open circles; C). The inset shows an example of a tangent (solid
55 circle and hatched line), for the 2.9-ms interval marked in other panels (B and C) by a
56 solid black circle. We used the range in slopes to characterise the magnitude of
57 frequency modulation throughout the call. The grey hatched line indicates a slope of
58 zero (C).

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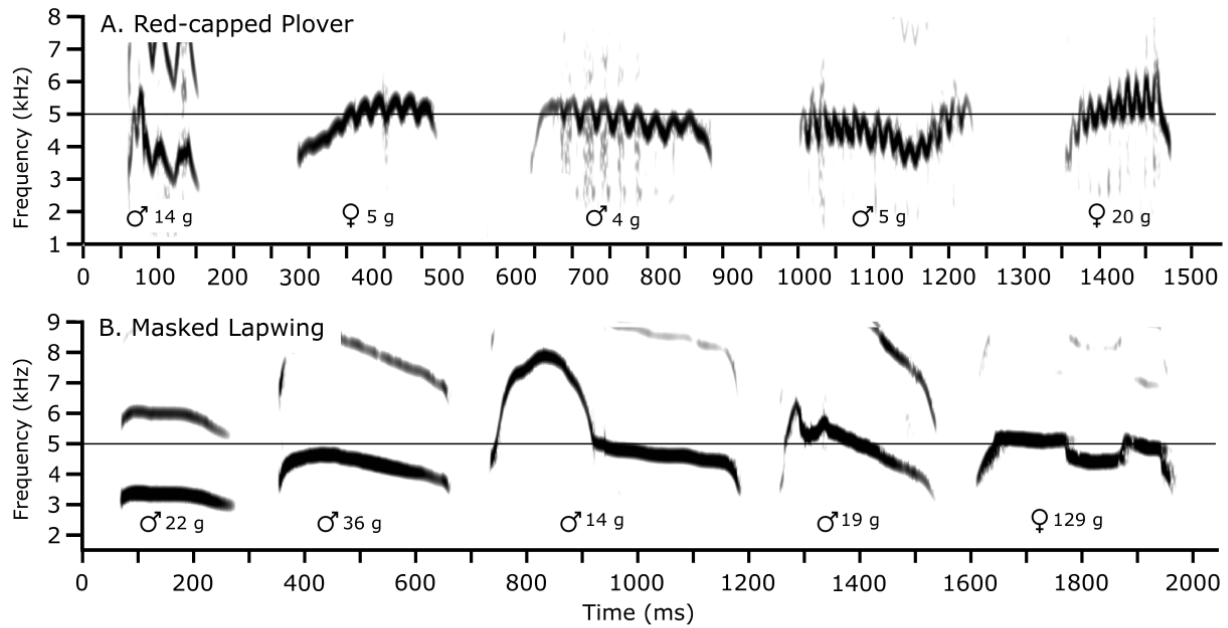
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61 Figure S2. The frequency distribution of log-transformed frequency modulation (rate of
62 change in dominant frequency) for Masked Lapwing chick calls.

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66 Figure S3. Chick distress calls differed substantially between Red-capped Plover (A)

67 and Masked Lapwing (B), particularly in the presence and extent of frequency

68 modulation (FM). Calls are ordered left-to-right by rate of FM for Plovers and by

69 increasing overall complexity for Lapwings.

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72 Table S1. Body measurements for all Red-capped Plover chicks within this study.

Date	Known age	Recording number	Chick ID	Sex	Brood number	Body mass	Head bill	Bill	Tarsus	Tarsus and toe	Recapture
3/01/2019	1.0	R350	chick 2	Male	1	4.5	22.6	17.6	19.42	33	
20/01/2019		R362	chick 2a	Female	3	4	24.12	7.6	19.02	34.5	
1/02/2019		R379	3691822	Male	4	11.3	29.43	10.78	22.35	40	
1/02/2019		R380 + 381	3691823	Male	5	8.5	29.41	10.62	23.96	41	
4/03/2019		Z240	3691820	Male	18	6.3	25.9	8.09	19.66	38	
1/02/2019	1.0	R382	3691824	Female	6	5.5	24.2	7.59	16.35	35	
22/03/2019		R410	3691820	Male	18	14.5	32.64	9.83	23.55	42	Y
1/02/2019	1.0	R383	3691825	Female	6	3.5	24.89	8.16	18.62	35	
11/02/2019	1.0	R391	3691827	Male	8	5	20.71	6.25	16.5	31	
11/02/2019		R394	3691835	Male	11	4.2	23.89	7.82	17.8	34	
11/02/2019		R393	3691829	Male	9	19.7	35.24	12	24.98	45	
18/02/2019		Z232	3691831	Female	14	8	27.59	9.3	20	40	
11/02/2019		R392	3691828	Male	12	5.1	23.37	7.31	18.65	36	
18/02/2019		Z233+Z234	3691832	Female	14	20.5	35.7	12.88	26.02	44.5	
4/03/2019		Z238	3691828	Male	12	21.8	33.73	10.91	24.99	45	Y
18/02/2019		Z230 +Z231	3691833	Female	13	19.7	35.13	11.31	25.42	42.5	
18/02/2019		Z229	3691834	Female	12	7.2	26.52	8.5	20.75	38.5	Y
18/02/2019		Z235	3691836	Male	15	11.5	29.96	10.1	20.44	39.5	
11/02/2019		R396	3691834	Female	12	5.3	23.68	7.3	19.3	46	
25/02/2019		Z236	3691828	Male	12	12.5	30.51	9.61	21.79	41	Y
4/03/2019		Z239	3693837	Male	17	7.9	26.88	8.79	22.6	42	
8/03/2019	1.0	R405	3691839	Male	19	3.8	23.83	7.74	19.15	46	
8/03/2019	1.0	R404	3691838	Male	19	3.6	25.24	7.55	18.88	36	
8/03/2019		R406	3691840	Male	18	9.7	27.34	8.85	19.98	38	Y
14/03/2019		R407	3691820	Male	18	9.1	29.14	10.8	20.46	39.5	Y
14/03/2019		R408	3691840	Male	18	8.2	29.23	9.19	21.67	44	Y
14/03/2019	7.0	R409	3691838	Male	19	4.8	26.7	8.15	19.15	37	Y

Date	Known age	Recording number	Chick ID	Sex	Brood number	Body mass	Head bill	Bill	Tarsus	Tarsus and toe	Recapture
22/03/2019		R411	3691840	Male	18	14.8	31.85	11.07	22.04	41	Y
16/12/2019	1.0	Z255	03691814	Male	24	4.6	21.79	7.1	16.51	33	
16/12/2019	1.0	Z254	03691815	Female	23	4.6	22.05	7.02	17.34	33	
16/12/2019	1.0	Z252	03691817	Male	22	6.5	24.22	7.65	17.92	34.5	
16/12/2019	1.0	Z251	03691818	Female	22	3.9	23.35	7.78	17.42	35	
16/12/2019	1.0	Z247	03691845	Male	20	4.8	22.98	17.94	16.83	34	
16/12/2019	1.0	Z250	03691846	Male	21	4.2	23.3	7.52	18.3	36	
16/12/2019		Z247	03691845	Male	20	4.8	22.98	17.94	16.83	34	
16/12/2019		Z250	03691846	Male	21	4.2	23.3	7.52	18.3	36	
16/12/2019		Z251	03691818	Female	22	3.9	23.35	7.78	17.42	35	
16/12/2019		Z252	03691817	Male	22	6.5	24.22	7.65	17.92	34.5	
16/12/2019		Z254	03691815	Female	23	4.6	22.05	7.02	17.34	33	
16/12/2019		Z255	03691814	Male	24	4.6	21.79	7.1	16.51	33	

74 Table S2. Body measurements for all Masked Lapwing chicks within this study.

Date	Known age	Recording number	Chick ID	Sex	Brood number	Body mass	Head bill	Bill	Tarsus	Tarsus and toe
2/08/2018	1.0	R63 + R64 + Z71	083- 24303	Male	1	18.2	37.7	11.89	27.51	59
2/08/2018	1.0	R65	083- 24304	Male	1	22.4	36	12.32	32.19	57.1
2/08/2018	1.0	R66	083- 24305	female	1	22.5	35.41	12.01	31.09	58
2/08/2018	1.0	R67	083- 24306	Male	2	22.4	35.09	11.02	28.76	55.5
2/08/2018	1.0	R68	083- 24307	female	2	21.1	36.07	11.31	30.33	59
2/08/2018	1.0	R69	083- 24308	female	2	22.2	35.6	11.65	28.99	58
2/08/2018	1.0	R71	083- 24310	Male	3	17	32.17	9.8	27.82	52
3/08/2018	1.0	R72	083- 24311	Male	4	21.5	33.2	10.47	28.3	55.5
3/08/2018		R76	083- 24312	female	5	45.4	47.29	19.21	33.49	64
3/08/2018	2.0	R84	083- 24313	female	6	21.8	37.98	13.79	21.15	59.5
3/08/2018	2.0	R78 + R81	083- 24314	Male	6	19.4	37.92	14.01	30.26	60
3/08/2018	2.0	R83	083- 24315	female	6	20.7	37.06	13.8	29.84	58
3/08/2018	2.0	R79 + R80 + R82	083- 24316	Male	6	19.5	36.81	12.95	29.64	59
3/08/2018		R85	083- 24317	female	7	23.9	42.95	16.42	29.66	60
3/08/2018		R86	083- 24318	female	7	23.1	41.6	15	30	59
3/08/2018		R87	083- 24319	Male	9	28	44.43	17.45	34.02	65
3/08/2018		R88	083- 24320	female	9	29	44.06	18.66	32.88	64
3/08/2018		R89	083- 24321	female	10	22.5	35.52	12.44	28.89	58
3/08/2018	2.0	R90	083- 24322	female	11	22.5	34.49	10.58	28.6	58
3/08/2018	2.0	R91	083- 24323	Male	11	21.5	36.6	11.91	31.11	60.5
3/08/2018		R93 + R94	083- 24325	Male	12	95	55.09	22.79	44.94	80
3/08/2018	7 or 8	R 96 + R100	083- 24326	Male	13	22.3	41.09	15.3	31.74	63
3/08/2018	7 or 8	R 97 +R99	083- 24327	Male	13	25.2	40.75	13.99	32.08	61
3/08/2018	7 or 8	R98	083- 24328	Male	13	17.9	41.69	15.6	32.14	60.5
3/08/2018	7 or 8	R101	083- 24329	female	13	26.5	42.09	14.9	32.21	60
3/08/2018	10 or 11	R102	083- 24330	female	14	37.4	46.45	17.85	36.6	68
3/08/2018	10 or 11	R103 + R106	083- 24331	Male	14	33.4	42.91	13.83	32.84	62
3/08/2018	10 or 11	R104	083- 24332	female	14	46.8	47.42	17.15	37.28	69.5
3/08/2018	10 or 11	R105	083- 24333	Male	14	44.9	47.3	17.48	N/A	68

Date	Known age	Recording number	Chick ID	Sex	Brood number	Body mass	Head bill	Bill	Tarsus	Tarsus and toe
6/08/2020	5 or 6	R107	chick 1d	Male	16	15.5	36.35	12.51	28.19	53
9/08/2018		R118	083- 24338	Male	17	63	51	21.58	39.18	72
9/08/2018		R119 + R121	083- 24339	female	17	73	52.75	22.67	43.7	76
9/08/2018		R120	083- 24340	female	17	65	52.91	23.76	40.65	73
9/08/2018		R123	083- 24341	female	18	18.6	37.19	12.85	29.97	59
9/08/2018		R126	083- 24342	female	18	20.7	37.43	12.39	31.69	58
9/08/2018		R132 + R133	083- 24345	female	19	24.3	37.9	13.8	31.79	62
9/08/2018		R134	083- 24346	Male	19	21.1	37.33	12.53	31.19	58
9/08/2018		R140	083- 24348	female	20	44.6	48.4	17	37.52	69
9/08/2018		R143	083- 24350	female	20	39.55	46.72	17.33	34.26	68
9/08/2018	3.0	R145	083-36151	female	21	23	39.11	14.67	34	62
9/08/2018	3.0	R146	083-36152	female	21	21.2	37.46	13.14	31.47	59.5
9/08/2018		R147	083-36153	Male	22	37	46.26	17.93	34.59	64
9/08/2018		R148	083-36154	Male	22	36.2	45	18.89	34.29	63
9/08/2018		R149	083-36155	female	22	34	44.79	18.35	35.83	63
10/08/2018	1 to 3	R154	083-36158	female	24	21.2	35.81	11.39	31	59
10/08/2018	1 to 3	R157 R158	083-36159	Male	24	19.5	37.45	12.4	29.66	56.5
10/08/2018	1 to 3	R159	083-36160	female	24	20.1	34.65	10.68	30.22	56
10/08/2018		R160	083-36161	female	25	19.4	38.43	14.25	32.69	61.5
10/08/2018		R161	083-36162	Male	25	18.5	38.31	14.71	30.04	58
10/08/2018		R162	083-36163	female	25	15.2	39.83	15.28	34.69	63.5
16/08/2018		R194 + 195	chick 1	Male	27	55	50.62	22.55	42.15	75
16/08/2018		R194	chick 2	female	27	53.9	48.25	19.5	39.3	70
23/08/2018		R208 + 209	083-36166	Male	29	43.5	45.68	16.62	35.89	65
23/08/2018		R210	083-36167	Male	29	49	46.96	19.24	36	63.5
23/08/2018		R211	083-36168	female	30	97	54.49	21.15	47.35	81
23/08/2018		R212	083-36169	female	30	97	53.81	21.3	46.83	80
23/08/2018		R213	083-36170	Male	31	36	43.25	15.61	33.59	62
23/08/2018		R214	083-36171	Male	32	87	54.79	24.55	44.7	80
23/08/2018		R215	083-36172	female	33	30.3	42.46	15	34.45	61
23/08/2018		R216	083-36174	Male	33	26.5	41.19	15	33.6	62
23/08/2018		R217	083-36175	female	33	33.5	42.46	15.78	35.01	64

Date	Known age	Recording number	Chick ID	Sex	Brood number	Body mass	Head bill	Bill	Tarsus	Tarsus and toe
23/08/2018	3.0	R221	083-36177	female	34	18.5	37.69	12.2	29.48	58
23/08/2018	3.0	R222	083-36178	female	34	20.2	38.2	13.05	30	57
23/08/2018	10.0	R223	083-36179	Male	35	25.5	40.26	15.29	31.45	57
23/08/2018	10.0	R224	083-36180	Male	35	35.3	44.81	17.4	33.7	64.5
24/08/2018		R228	083-36181	Male	36	58.8	48.97	19.39	38.07	71
24/08/2018		R229	083-36182	female	36	109	59.14	26.58	48.16	85
24/08/2018		R230	083-36183	Male	36	110	58.08	25.71	49.65	83.5
24/08/2018	14.0	R231	083-36184	Male	37	56.1	47.83	17.49	37.34	68.5
24/08/2018		R232	083-36185	Male	38	83	53.84	22.21	35	80
24/08/2018		R233	083-36186	female	38	47	48.78	20.5	34.85	65
12/09/2018	13 to 14	R318	chick 1a	female	39	41.8	46.3	17.92	35.11	67
12/09/2018		R321	chick 1b	female	41	29	41.3	15.75	32.68	59
12/09/2018		R322	chick 1c	Male	42	30	43.21	18.42	34.49	62
12/09/2018		R323	chick 2a	Male	42	24.5	42.37	15.76	33.8	61.5
20/09/2018		T56	083-36188	female	44	35	42.81	16.81	32.84	61
20/09/2018		T57	083-36189	female	44	28.7	42.02	17.3	22.33	61.5
20/09/2018		T58	083-36190	Male	45	32.5	45	18.35	32.19	61
20/09/2018		T59 + 60	083-36173	female	46	44	47.41	18.72	36.13	66.5
20/09/2018		T61, 62, 63 + 64	083-36191	Male	46	62.8	49.7	19.38	40.22	71
20/09/2018		T65	083-36192	Male	46	41	46.18	17.04	34.79	66
20/09/2018		T69	083-36196	female	48	50.5	46.54	17.91	36.22	64.5
20/09/2018		T67 + 70	083-36194	Male	48	48.3	47.38	19.44	37.72	70
20/09/2018		T68	083-36195	Male	48	47.6	47.63	17.76	37.49	67
20/09/2018		T71	083-36197	Male	49	177	62.84	28.29	59.84	97
20/09/2018		T75	083-27551	female	50	86	55.43	24.45	47.84	81.5
20/09/2018		T72	083-36198	Male	50	55.4	49.3	20.71	39.3	69
20/09/2018		T73	083-36199	Male	50	89	52.61	21.25	46.68	81
21/09/2018		T76	083-27552	female	51	129	59.96	26.75	52.12	92
21/09/2018		T77	083-27553	Male	51	124	59.5	27.34	55.69	94
21/09/2018		T78	083-27554	Male	52	39.7	45	16.92	36.64	68
21/09/2018		T79	083-27555	Male	53	45.2	44.58	15.5	34.99	65.5
21/09/2018		T81	083-27557	Male	55	31.4	45.38	18.49	33.32	61

Date	Known age	Recording number	Chick ID	Sex	Brood number	Body mass	Head bill	Bill	Tarsus	Tarsus and toe
21/09/2018		T82	083-27558	Male	56	44.9	47.5	18.54	36.98	67
21/09/2018		T83	083-27559	female	57	133	58.4	25.23	51.11	88
21/09/2018		T84	083-27560	Male	58	49.7	45.41	18.25	35	66

75

76 Table S3. Results of the generalised linear mixed model investigating the relationship
77 between frequency modulation of Masked Lapwing calls with outliers removed (> 1.5
78 times the interquartile ranges below the first or above the third quartile) and body mass
79 (reciprocal transformation) and sex (reference category = female). We specified a
80 Toeplitz covariance structure, and chick identity nested within brood identity was
81 included as the random effect for all analyses. Estimates are presented as estimates of
82 coefficients \pm standard error for fixed effects, and variance \pm standard deviation for the
83 random effect of identification nested within Brood ID. The probability distribution was
84 Gaussian and we used an identity link. The response variable was logarithmically
85 transformed. * = to aid interpretation, note that the reciprocal transformation reflects the
86 sign of coefficients.

Species	Response variable	Model terms	Estimates	<i>z</i>	<i>P</i>
		Body mass*	5.626 \pm 0.873	6.450	< 0.001
Masked Lapwing	Frequency modulation <i>n</i> = 6456 calls	Sex	-0.091 \pm 0.027	-3.330	< 0.001
		Identification: Brood ID	0.014 \pm 0.119	NA	NA

87

88 Table S4. Results of the generalised linear mixed model investigating the relationships
 89 of body mass (reciprocal transformation), sex (reference category = female), and call
 90 saturation (reference category = not saturated) with call entropy for both species. We
 91 specified a Toeplitz covariance structure, and chick identity nested within brood identity
 92 was included as the random effect for all analyses. Estimates are presented as
 93 estimates of coefficients \pm standard error for fixed effects, and variance \pm standard
 94 deviation for the random effect of identification nested within brood ID. The probability
 95 distribution was Gaussian and we used an identity link. * = logarithmically transformed
 96 data. ** = to aid interpretation, note that the reciprocal transformation reflects the sign of
 97 coefficients.

Species	Response variable	Model terms	Estimates	<i>z</i>	<i>P</i>
Red-capped Plover	Entropy* <i>n</i> = 2365 calls	Body mass**	-0.069 \pm 0.047	-1.455	0.146
		Sex	0.003 \pm 0.007	0.413	0.679
		Saturation	-0.013 \pm 0.001	-16.810	< 0.001
		Identification: Brood ID	0.000 \pm 0.017	NA	NA
Masked Lapwing	Entropy <i>n</i> = 6456 calls	Body mass**	1.810 \pm 0.373	4.850	< 0.001
		Sex	-0.003 \pm 0.011	-0.280	0.780
		Saturation	-0.020 \pm 0.002	-9.610	< 0.001
		Identification: Brood ID	0.003 \pm 0.055	NA	NA

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