


Short Communication

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

KRISTAL N. KOSTOGLOU,^{*1,2} 

EDWARD H. MILLER,³ 

MICHAEL A. WESTON^{1,2}  & DAVID R. WILSON⁴ 

¹Deakin University, Geelong, VIC, Australia

²School of Life and Environmental Sciences, Deakin University, Burwood Campus, 221 Burwood Highway, Burwood, VIC, 3125, Australia

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

⁴Psychology Department, Memorial University, St. John's, NL, Canada

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 oediacnemus* 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,

*Corresponding author.

k.kostoglou@research.deakin.edu.au

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.

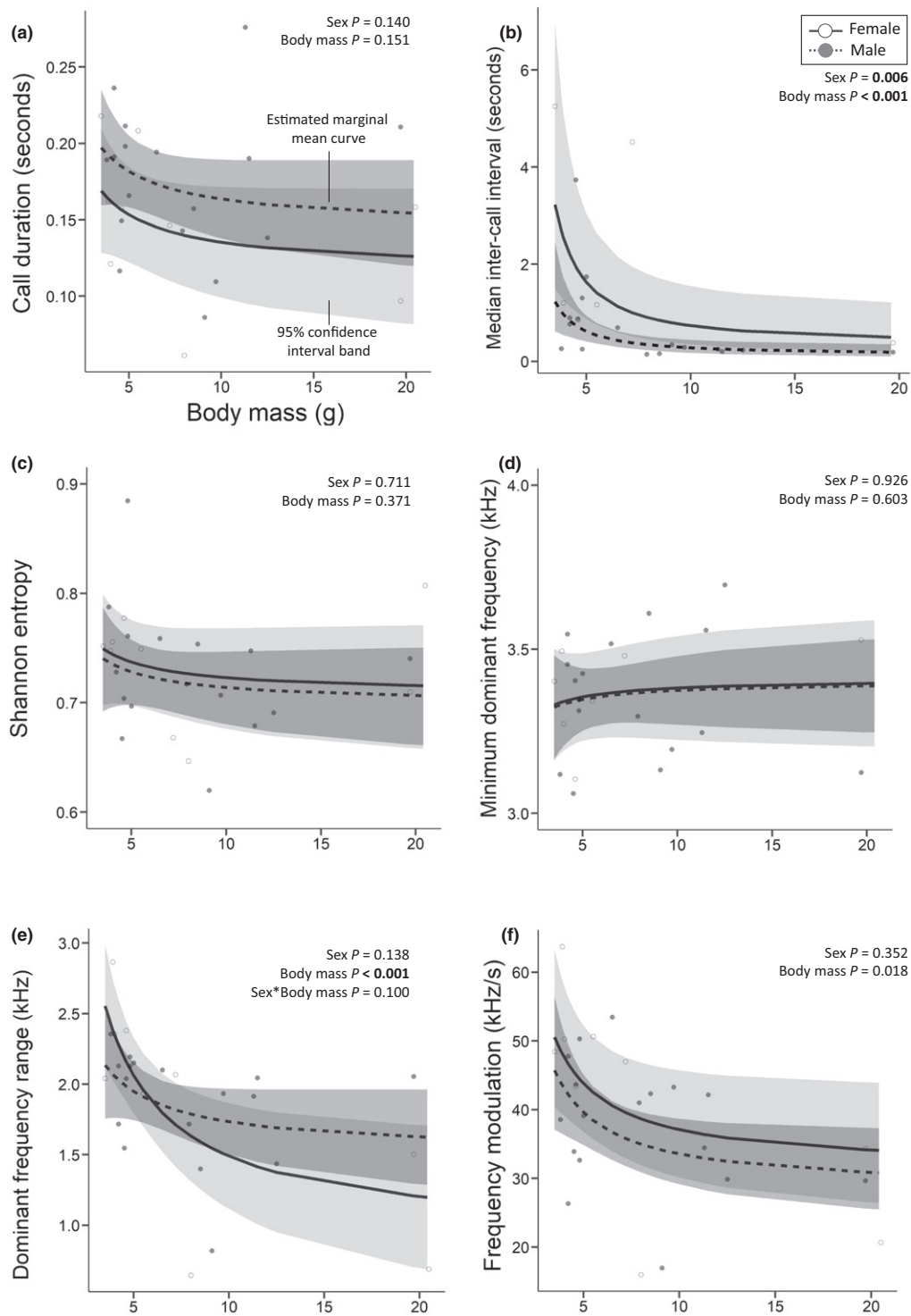


Figure 1. For Red-capped Plovers, call duration did not vary with body mass or sex (a), but inter-call intervals (ICIs) decreased with increasing body mass and were shorter in males (b). Entropy and minimum dominant frequency did not vary with body mass or sex (c,d). Dominant frequency range decreased 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.

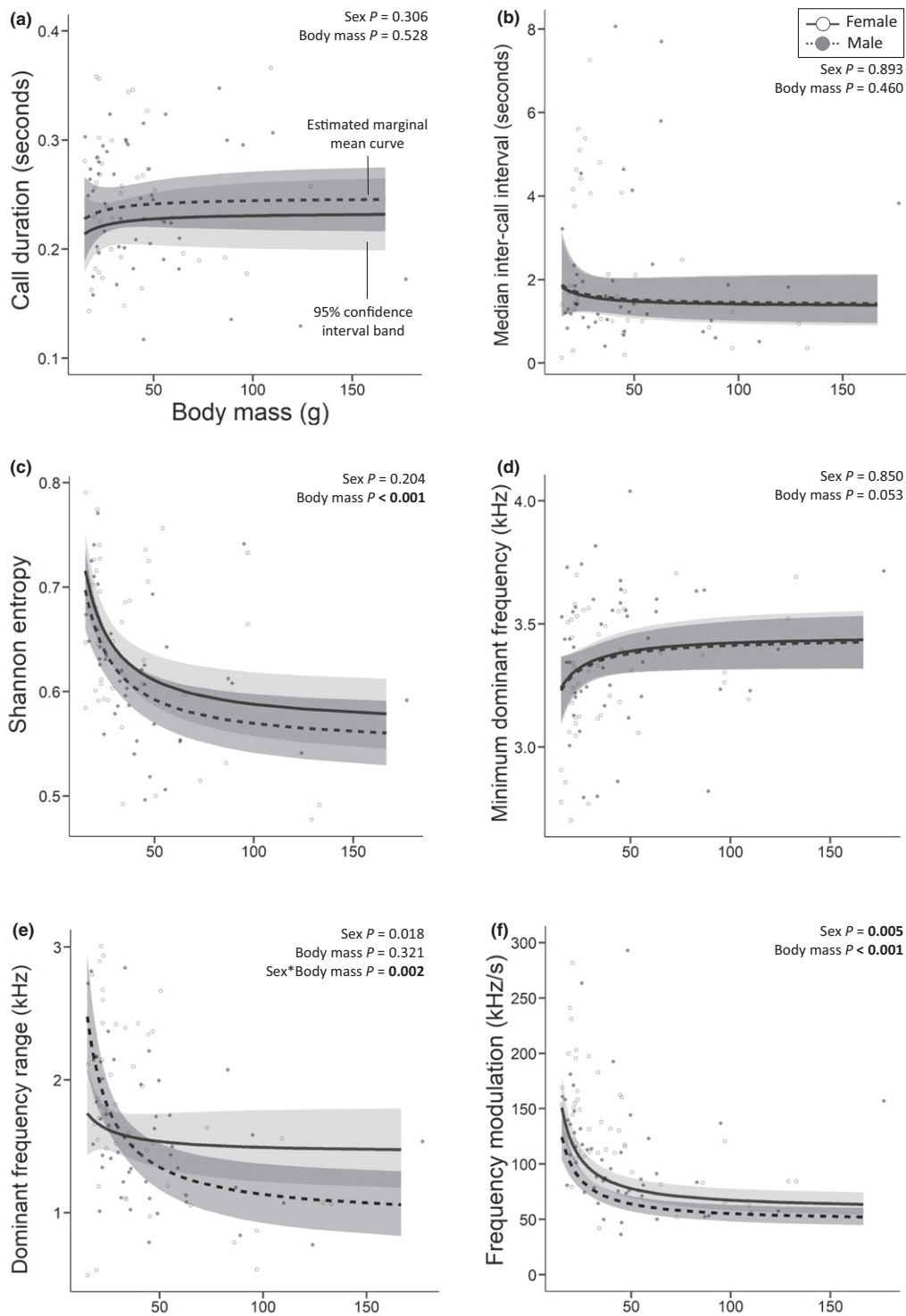


Figure 2. For Masked Lapwings, call duration and inter-call intervals (ICIs) did not vary with body mass or sex (a,b), but entropy decreased with increasing body mass (c). Minimum dominant frequency did not vary with body mass or sex (d), but dominant frequency range decreased with body mass and the 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.

FUNDING

Holsworth Wildlife Research Endowment. Open access publishing facilitated by Deakin University, as part of the Wiley - Deakin University agreement via the Council of Australian University Librarians.

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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Received 31 August 2021;
Revision 30 January 2022;
revision accepted 9 February 2022.
Associate Editor: Phil Battley.

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.