

Nestling Begging Calls Resemble Maternal Vocal Signatures When Mothers Call Slowly to Embryos

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Submitted July 21, 2022; Accepted July 11, 2023; Electronically published January 4, 2024

Online enhancements: tables.

ABSTRACT: Vocal production learning (the capacity to learn to produce vocalizations) is a multidimensional trait that involves different learning mechanisms during different temporal and socioecological contexts. Key outstanding questions are whether vocal production learning begins during the embryonic stage and whether mothers play an active role in this through pupil-directed vocalization behaviors. We examined variation in vocal copy similarity (an indicator of learning) in eight species from the songbird family Maluridae, using comparative and experimental approaches. We found that (1) incubating females from all species vocalized inside the nest and produced call types including a signature “B element” that was structurally similar to their nestlings’ begging call; (2) in a prenatal playback experiment using superb fairy wrens (*Malurus cyaneus*), embryos showed a stronger heart rate response to playbacks of the B element than to another call element (A); and (3) mothers that produced slower calls had offspring with greater similarity between their begging call and the mother’s B element vocalization. We conclude that malurid mothers display behaviors concordant with pupil-directed vocalizations and may actively influence their offspring’s early life through sound learning shaped by maternal call tempo.

Keywords: incubation call, introductory notes, Maluridae, maternal effects, pupil-directed vocalization, vocal production learning.

Introduction

Vocal production learning is a type of social learning in which vocal signals are “modified in form as a result of experience with those of other individuals” (table 1 in Janik and Slater 2000, p. 2). Such learned vocal signals have evolved as adaptations to enhance survival and reproductive success across a range of sociobiological and ecological challenges faced by animals (Carouso-Peck et al. 2021). Despite its many potential fitness benefits, the capacity to learn to produce new vocalizations occurs only in a handful of mammalian and avian taxa (Slater 1989; Jarvis 2019; Searcy et al. 2021), with most research focused on a few model species (Carouso-Peck et al. 2021). The current widely accepted view is that vocal production learning occurs along a continuum and may involve multiple learning processes (Petkov and Jarvis 2012; Lattenkamp and Vernes 2018; Wirthlin et al. 2019; Martins and Boeckx 2020; Searcy et al. 2021; ten Cate 2021). This perspective posits vocal learning as a multidimensional trait, which can be deconstructed into several key dimensions to help understand its underlying mechanisms (Vernes et al. 2021). Specifically, proposed dimensions include the copying of auditory models (e.g., accuracy of copying), degree of change (e.g., type and breadth of learning), and timing (e.g.,

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when learning takes place; Vernes et al. 2021). Despite considerable research, it remains unclear at which life stages animals are capable of vocal learning and also whether or how the mechanisms that enable vocal production learning early in life differ from those that allow production learning later in life (Vernes et al. 2021).

In vocal learners, sound exposure and the social context of sound exposure can affect neural development and vocal copy similarity (Sakata and Yazaki-Sugiyama 2020). However, recent experiments have demonstrated embryological onset of these pathways, with prenatal sound exposure associated with altered neural organization in songbird embryos (Rivera et al. 2019; Antonson et al. 2021) and postnatal differences in vocal learning (Colombelli-Négrel et al. 2012; Katsis et al. 2018). The Australian zebra finch (*Taeniopygia castanotis*) is a model system for the study of songbird vocal learning (Hauber et al. 2021a). For example, zebra finch embryos and nestlings exposed to conspecific calls showed greater *ZENK* immediate early gene activity relative to silence as control (Rivera et al. 2019), and the same embryos showed reduced genome-wide methylation in their auditory forebrain when exposed to conspecific heterospecific songs (Antonson et al. 2021). During the nestling stage, researchers found adultlike neural representation of species-specific songs in the auditory forebrain of zebra finch nestlings (Schroeder and Remage-Healey 2020). The mechanistic pathways by which early-life sound exposure influences song learning have yet to be determined. However, these previous findings make it plausible that embryo and nestling brains could benefit from and be shaped by early sound exposure if these vocalizations draw the attention of pupils—for example, via a cardiac orientation response (Hauber et al. 2002; Colombelli-Négrel et al. 2014; Colombelli-Négrel et al. 2021)—and consequently alter their gene activity and vocal copy similarity.

Vocal tutors may adjust their social response, vocalization behavior, and/or vocalization characteristics when interacting with pupils, which may make the vocalizations easier to memorize and imitate by the pupil (Golinkoff et al. 2015; Araguas et al. 2022; Faust and Goldstein 2022). Specifically, tutors may produce pupil-directed vocalizations (Carouso-Peck and Goldstein 2019, 2021; Carouso-Peck et al. 2020; Hauber et al. 2021a), which are characterized by slower tempos and the presence of introductory notes and syllables (Grieser and Kuhl 1988; Chen et al. 2016; Faust et al. 2020). Pupil-directed vocalizations have been described in various vocal learning taxa, including humans (Snow 1977; Gleitman et al. 1984), cetaceans (Burnham and Duffus 2020), bats (Fernandez and Knörnschild 2020), and songbirds (Chen et al. 2016). Zebra finches use parental gestural and vocal feedback (Carouso-Peck et al. 2020; Faust and Goldstein 2022) and produce offspring-directed songs

(Chen et al. 2016) to enhance vocal learning. The pupil-directed song of adult males has more introductory notes and longer time intervals between motifs (song phrases) compared with undirected songs (Chen et al. 2016). Some of these modifications (e.g., longer intervals between motifs) are unique to offspring-directed songs and do not occur when male songs are directed toward adult females. As a result of these vocal changes, offspring-directed songs are better able to hold the attention of zebra finch young (Chen et al. 2016). Among mammals, only in humans do we have evidence for pupil-directed vocalization behavior by adults toward embryos: human mothers vocalize to their fetus, and fetuses respond to the maternal voice (Hepper et al. 1993; Fifer and Moon 1994). It is not clear which factors influence the magnitude of fetal response to sound, which calls for more research into how maternal vocalization characteristics and maternal-fetal interactions influence human vocal learning (Carvalho et al. 2019).

The superb fairy wren (SFW; *Malurus cyaneus*), a member of the songbird family Maluridae, has in recent years become a model system for the study of prenatal maternal calls in relation to offspring sound learning in ovo (Colombelli-Négrel et al. 2012, 2021). This research demonstrated that calls can also be learned during early embryological stages. Incubating females produce incubation calls while inside the nest; each call has duration of ~1.2 s and contains two element types (denoted as A and B elements). The B element is considered a signature element, since its spectral structure appears to differ consistently between females within a population (Colombelli-Négrel et al. 2012). After hatching, nestlings produce a begging call whose structure resembles the B element from their mother's incubation call (Colombelli-Négrel et al. 2012). In a field experiment, offspring that were cross-fostered during incubation produced their foster mother's B element as their begging call after hatch, consistent with prenatal sound learning (Colombelli-Négrel et al. 2012). On the basis of in ovo heart rate (HR) measurements, SFW embryos can habituate and dishabituate to calls from different females (Colombelli-Négrel et al. 2014), and embryos with stronger prenatal call discrimination scores (i.e., stronger response during a dishabituation test) have larger vocal repertoires as fledglings (Kleindorfer et al. 2018). There is also growing evidence from multiple malurid species that mothers may help shape the adaptive sound-learning trajectories of their offspring, beginning in the egg. For example, hatchling red-backed fairy wrens (RBFW; *Malurus melanocephalus*) with higher vocal copy accuracy of the learned begging call are fed more by the attending parents (Colombelli-Négrel et al. 2016), and *M. cyaneus* hatchlings with higher begging call accuracy are less likely to be mistaken for a brood parasitic cuckoo (Colombelli-Négrel et al. 2012; Kleindorfer et al. 2014a).

To better understand the possible developmental effects of early-life sound experience and determine whether pupil-directed vocalizations could occur toward embryos, we need cross-species comparisons of parental vocalization behavior in relation to offspring responsiveness to sound and vocal learning. We aimed to narrow this gap in knowledge by analyzing the vocalization behavior of incubating females in Maluridae, using a combination of comparative and experimental approaches. First, we describe the prevalence and acoustic characteristics of in-nest calls produced by incubating females in eight malurid species. This songbird family is characterized by uniparental female incubation, which allowed us to document the occurrence and potential impacts of female vocalization behavior on sound learning during early life stages (Lattenkamp and Vernes 2018). Second, in the SFW, we experimentally test how embryos respond to calls of different elemental composition, including the presence and number of A and B elements. We predict a stronger response to B elements (i.e., the signature element) over A elements (i.e., the introductory element). Third, across eight malurid species, we investigate which aspects of maternal calls (e.g., number of introductory notes, number of elements, element rate—i.e., number of elements per second) predict vocal similarity between the female B element and hatchling calls. Both call tempo (here, element rate) and introductory notes have been identified as components of pupil-directed vocalizations that enhance attention in pupils (Grieser and Kuhl 1988; Chen et al. 2016). If there has been selection on maternal traits associated with the production of offspring-directed vocalizations, we expect to find a positive effect of call composition, number of introductory notes, and/or element rate on embryo responses to call elements and on vocal similarity in hatchlings. Should maternally guided prenatal vocal learning indeed be occurring, this highlights new developmental pathways that could produce variable and locally suited phenotypes.

Methods

Study Species and Study Sites

During the period 2007–2020, we recorded 624 in-nest vocalizations of 125 females from eight Maluridae species and 12 study populations in Australia (for details, see table S1; fig. A1). The study species were (1) superb fairy wren (SFW; *Malurus cyaneus*), (2) splendid fairy wren (SPLFW; *M. splendens*), (3) red-backed fairy wren (RBFW; *M. melanocephalus*), (4) white-winged fairy wren (WWFW; *M. leucopterus*), (5) red-winged fairy wren (RWWF; *M. elegans*), (6) variegated fairy wren (VFW; *M. lamberti*), (7) purple-crowned fairy wren (PCFW; *M. coronatus*), and a related malurid, the (8) thick-billed grass-wren

(TBGW; *Amytornis modestus*). In all of the species, the incubation and chick-feeding phases each last ~12–14 days. From a previous study conducted during 2007–2014 on SFWs and RBFWs, we observed in-nest calls during the late incubation phases by all females (Colombelli-Négrel et al. 2012, 2016). For these species, we have detailed observations of nests using video and audio recorders, which show that the female produces in-nest calls to the eggs in the absence of any other bird visible within 10 m of the nest. The onset of female calling to eggs is generally around day 10 of incubation. Across species, we cannot say with certainty when females stop vocalizing inside the nest, although calling in SFWs usually ends on the day of hatching, and in RBFWs it can persist until day 6 after hatching but with fewer calls per hour compared with the incubation phase (Colombelli-Négrel et al. 2016).

In-Nest Recordings of Calls and Calling Behavior

We searched each study site for nests in known fairy wren or grass-wren territories. Nests found during the building stage were checked every 1–3 days to determine the onset of laying and incubation. For nests located during the incubation stage, we estimated egg age using candling and later verified these estimates by back calculating from the hatch date. We recorded in-nest vocalizations 10–13 days after the onset of incubation ($N = 125$ nests) and once again when nestlings were 3–5 days old ($N = 86$ nests, a reduced sample size due to nest losses from predation; sample size per species in table S1). We selected this sampling window because previous research showed that SFW females begin calling to embryos from incubation day 10 until hatch (day 14), and embryos do not show evidence for sound discrimination before incubation day 10 (Colombelli-Négrel et al. 2014; D. Colombelli-Négrel and S. Kleindorfer, unpublished data). Vocalizations were recorded with the following devices: (1) Olympus linear LS-10 handheld PCM recorder (sample rate of 24 kHz in 16-bit PCM format; for RBFW, VFW), (2) Wildlife Acoustics song meter SM2 autonomous recording unit (24 kHz in 16-bit PCM format; Wildlife Acoustics, Concord, MA; for RBFW, VFW); (3) Zoom H4n handy recorder (48 kHz in 16-bit PCM format; for RWWF, WWFW, SFW, TBGW, SPLFW), and (4) Zoom H5n handy recorder (48 kHz in 16-bit PCM format; for PCFW). The microphones were placed approximately 30 cm under the nest and recorded for a minimum of 2 h. Recording usually took place in the morning between 0500 and 1100 hours locally. The recordings were saved as WAV sound files, transferred to an Apple Mac Pro, and visualized as spectrograms using Amadeus Pro 1.5 (HairerSoft) and Raven Pro 1.5 (K. Lisa Yang Center for Conservation Bioacoustics 2014). We generated spectrograms using the Hann algorithm (16-bit sample format; discrete Fourier

transform = 512 samples; frequency resolution = 135 Hz; time resolution = 5.33 ms; frame overlap = 50%).

Variation in In-Nest Calls. We visually scanned spectrograms of all incubation recordings for the presence of maternal in-nest calls and all nestling recordings for the presence of nestling begging calls. We defined a maternal in-nest call as a call that (1) is approximately 1–2 s long and contains 1–4 element types (A–D; see “Results”;

fig. 1); (2) is produced when the female was in the nest during incubation or shortly after hatching, verified at SFW, RFWF, and TBGW nests using a GoPro camera (GoPro, San Mateo, CA) placed near the nest entrance and otherwise confirmed from the acoustic properties of the recordings; and (3) contains an element similar in structure to that of their nestlings’ begging call (referred to as “B element”; see “Results”; fig. 1; table 1). For RFWF, TBGW, and PCFW, 12 females (9% of all

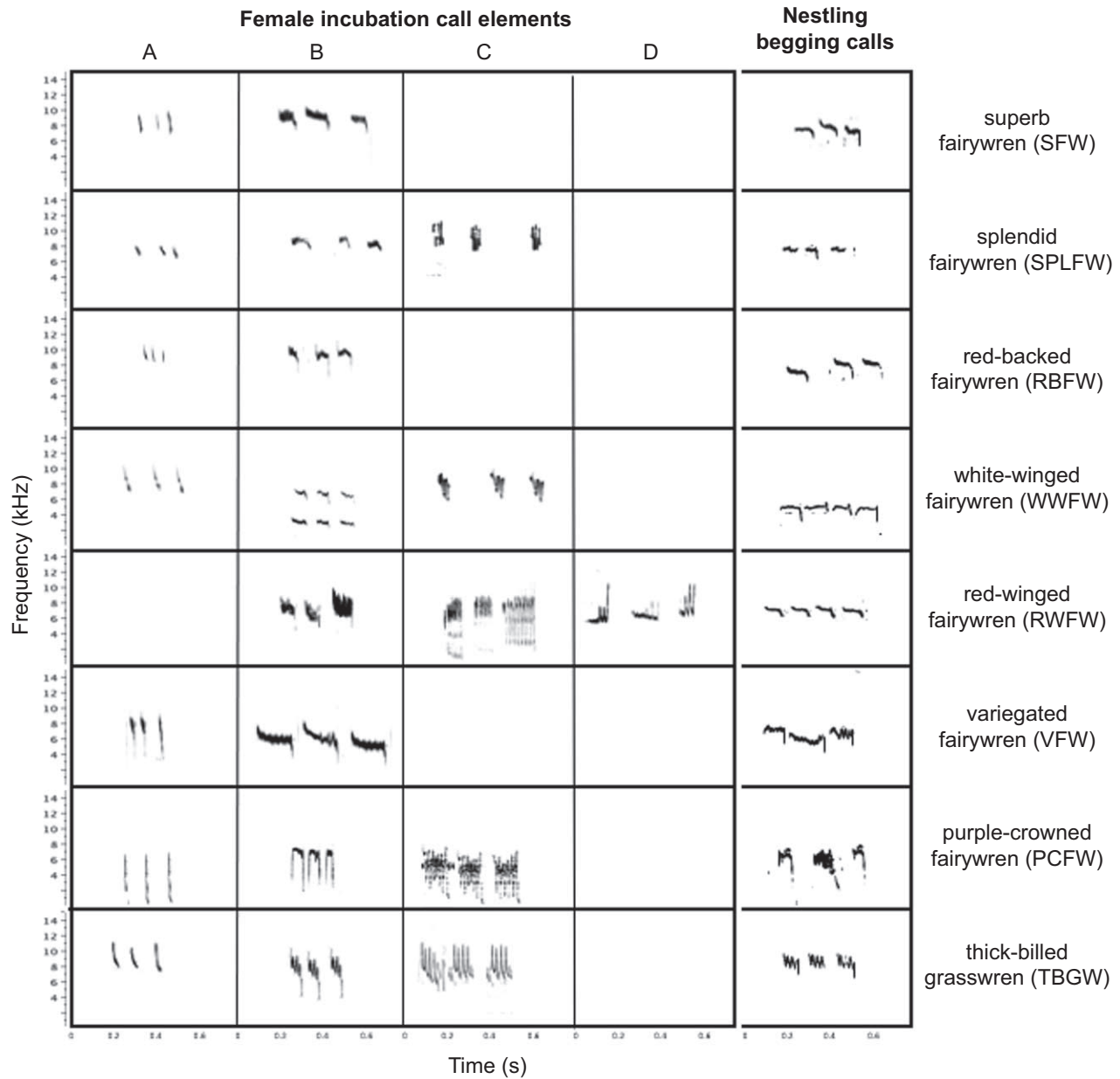


Figure 1: Element types (A–D) observed in female in-nest calls (*left*) and representative examples of nestling begging calls at different nests from unrelated offspring (*right*) recorded from eight Maluridae species. The acoustic characteristics used to classify element types are described in table 1.

Table 1: Acoustic characteristics used to classify element types from eight Maluridae species

Element type	Characteristics
A	A single stroke pattern high to low frequency, less than .1 s long, frequency range across species is 1–11 kHz
B	A single low-high-low modulation in frequency in a waveform pattern, followed by a downward stroke, at least .1 s long and resembles the shape of the begging call produced by nestlings, frequency range across species is 1–12 kHz
C	A single low-high-low modulation in frequency in a waveform pattern, at least .1 s long and has a buzzy sound, frequency range across species is 2–12 kHz
D	A single high-low-high modulation in frequency in an upward waveform pattern, at least .1 s long and found only in red-winged fairy wren calls, frequency range is 6–10 kHz

females in these three species; six RFWF, one TBGW, and five PCFW) produced maternal in-nest calls both with and without B elements. In this case, we considered a call without B elements as a maternal in-nest call if it followed criteria 1 and 2 and contained other elements that occurred as part of the maternal in-nest calls (B element plus other elements) of other females of the same species. We produced an element library of the different element types in the maternal in-nest calls per female per species (table 1; fig. 1). Element types were identified by three researchers through visual inspection of their spectrograms based on structural similarities and frequency and temporal modulations, following previously described methods for fairy wren song elements (see Dalziel and Cockburn 2008; Greig and Pruett-Jones 2008; Kleindorfer et al. 2013; Colombelli-Négrel et al. 2016). We conducted repeatability assays across the three researchers to ensure that element categories were valid and consistent (see also Evans and Kleindorfer 2016). All of the elements within a maternal in-nest call were identified and categorized according to our element library (table 1; fig. 1).

We calculated the number of calls per hour and then randomly selected up to five (average 4.93 ± 0.03 calls per female; range: 3–5) maternal in-nest calls per female and noted the duration, number of elements, and element types in each call. This allowed us to calculate the following in-nest call characteristics: (1) number of elements and element types per call, (2) element rate (number of elements per second), (3) number of introductory notes, and (4) proportion of B elements out of the total number of call elements. To be consistent with previous literature, here “element” refers to “a single trace on the spectrogram” (Catchpole and Slater 2008), “element type” refers to the specific element produced (Colombelli-Négrel et al. 2012), and “introductory notes” refers to non-B elements that occur before the first B element.

Experiment: Element Type and Number of A Elements. In SFWs, we experimentally tested whether an embryo’s response to call playback is influenced by the elemental composition of the call. We first generated artificial play-

back stimuli consisting of five elements using one or two element types and then broadcast these calls to fairy wren embryos. In our 2014 trials, we used incubation calls from eight different females (recorded in 2012), and in our 2022 trials, we used incubation calls from seven different females (recorded in 2020); we selected five unique A and B elements with high signal-to-noise ratio from each female ($N = 10$ unique elements per female). We then created eight (2014) and seven (2022) different playbacks, each composed of different A and B elements of one female only. In our 2014 trials, calls comprised either five A elements (AAAAA) or five B elements (BBBBB); embryos were exposed to either AAAAA only ($N = 14$ embryos) or BBBBB only ($N = 13$ embryos). Hence, we compared the embryos’ response to playback of five B elements versus five A elements to test whether embryos respond more strongly to one element type over another. In our 2022 trials, calls were a combination of A and/or B elements beginning with 0–5 A elements (0 = BBBBB, 1 = ABBBB, 2 = AABBB, 3 = AAABB, 4 = AAAAB, 5 = AAAAA), and embryos were exposed to all six call types in a randomized order, with each trial separated by 10 s ($N = 96$ trials using 16 embryos). Hence, we measured the embryos’ response when exposed to five-element calls with varying numbers of introductory A elements. The call stimulus was kept at five elements with a 0.2-s interelement interval for all playback trials so that differences in embryo response could not be attributed to stimulus duration or number of elements. Each embryo’s response to call playback (Hauber et al. 2002; Colombelli-Négrel et al. 2014, 2021) was measured as its change in HR (Δ HR), using a digital egg monitor (Buddy Egg Monitor, Vetric Services). This digital HR method has been independently validated for measuring response to stimuli in avian embryos (Pollard et al. 2016). In each embryo playback trial (see fig. 2), we (1) measured baseline HR (pre-HR), (2) exposed embryos to one call comprising a combination of A and B elements, and (3) measured HR during the second after call exposure (post-HR). On average, an incubation call has a duration of 1.2 s; we created the stimulus tracks so that the call stimulus

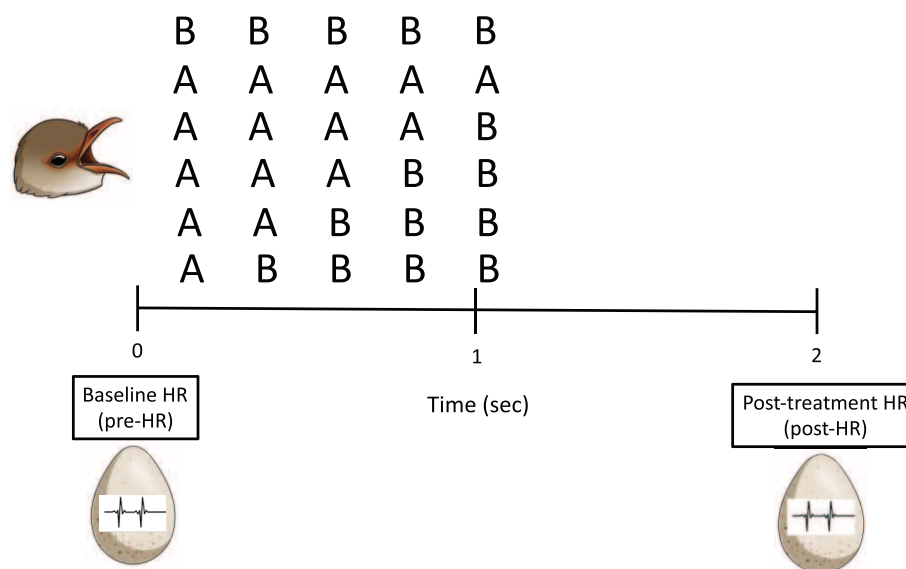


Figure 2: Schematic representation of the prenatal playback experiment to test the effect of element type and call composition on heart rate (HR) response in superb fairy wren (*Malurus cyaneus*) embryos. We recorded the baseline HR (pre-HR), then broadcast an artificial incubation call comprising five elements for duration of 1.2 s. We measured the embryo's HR response to treatment during the second following the last element exposure (post-HR). In 2014, calls comprised either five A elements (AAAAA) or five B elements (BBBBB); in 2022, calls were a combination of A and/or B elements beginning with 0–5 A elements (see “Methods”).

was presented during seconds 0 and 1, and we measured the response during second 2 after the final stimulus exposure during second 1 (the Buddy HR device displays HR per second). The embryos' response to the playback was quantified as their ΔHR (post-HR minus pre-HR), calculated using the HR value displayed on the device (Pollard et al. 2016).

Nestling Vocal Copy Similarity. To calculate copy similarity in all eight fairy wren species, we extracted two to five B elements per female (one per maternal in-nest call analyzed above) during incubation and two to five nestling begging calls (3–5 days old) per nest during the feeding phase, following Colombelli-Négrel et al. (2012). For each nest, the number of nestling begging calls was similar to the number of extracted maternal in-nest B elements (mean $\pm$ SE for both mother and nestling = 4.92 ± 0.04). Females in all of the eight species produced a B element (fig. 1), and this maternal B element was the reference call against which we compared nestling begging calls. Maternal and nestling elements were selected from calls with minimal background noise and, for nestling calls, when only one individual was calling. We then used the spectrographic cross-correlation (SPCC) function in Raven Pro 1.5 (e.g., Hauber et al. 2021b) to assess vocal similarity between the maternal B element during incubation and the nestling B element during feeding. SPCC quantifies the similarity between calls by

sliding two spectrograms past each other in time increments and generating a maximum correlation coefficient (range: 0–1) to represent their greatest overlap (Baker and Logue 2003). For each nest, a measure of vocal copy similarity was then derived as the average correlation coefficient between a female's B element during incubation and her offspring's B element after hatch. To minimize the influence of ambient noise in the recordings, we conducted the SPCC analysis with a band-pass filter between 2 and 16 kHz.

Statistical Analyses

Variation in In-Nest Calls. To compare how maternal in-nest calls varied among species, we ran a total of five generalized linear models (GLMs) and generalized linear mixed models (GLMMs) with our five nest call characteristics (number of calls per hour, number of elements per call, element rate, number of introductory notes, and copy similarity) as response variable and species as a fixed factor. Nestling vocal copy similarity (Gaussian distribution) and the average number of calls per hour (Poisson distribution) for each female were fitted in GLMs. The number of elements and introductory notes per call (Poisson distribution) and element rate (Gaussian distribution) were fitted using GLMMs, with female identity as a random intercept to account for repeated observations from the same female.

Because we were explicitly interested in interspecific differences and we had replicate populations for only two of the eight species examined (i.e., between-population and between-species variation were largely confounded), it was not feasible to additionally account for nonindependence at the population level. However, randomizing across 1,000 models with one randomly selected population per species did not qualitatively change our results (table S2). The number of calls and elements per call showed some evidence for overdispersion (dispersion parameter = 1.5 and 6.2, respectively), which was accounted for using an observation-level random intercept (number of elements) or a quasi-Poisson distribution (number of calls). There were no nests with zero calls. Every female produced calls with B elements, but sometimes (21 of 581 calls) a female produced a call without a B element. Calls also differed in the presence or absence of the other element types. Therefore, we retained calls without a B element, as otherwise it starts to become haphazard which calls we include or exclude. The average number of elements in a female's call with B elements (8.0 ± 1.2) and without B elements (7.6 ± 1.0) was comparable.

Experiment: Element Type and Number of A Elements. To test whether embryos responded to our maternal playbacks, we ran two GLMMs with the embryos' Δ HR as the response variable (Gaussian distribution). Our first model, using data from our 2014 experiments, compared the embryos' Δ HR (beats per minute) following exposure to five B elements (BBBBB) versus five A elements (AAAAA). This model included element type (A or B) as a fixed effect, nest ID as a random effect, and a zero-inflation parameter applying to all observations ($\text{ziformula} = \sim 1$). Our second model, using data from our 2022 experiments, tested whether embryos' HR response to playback was predicted by variation in the number of A elements, with the constraint that A elements always preceded a B element, if there was one. This model included number of A elements (0–5) as the continuous fixed effect, egg ID as a random effect, and a single zero-inflation parameter applying to all observations. In this model the residuals were leptokurtic so did not fully satisfy assumptions of normality. Therefore, we repeated this analysis using a GLMM (with a logit link function and a binomial error distribution) that treated the response variable as a binary outcome in which HR either decreased ($\Delta\text{HR} < 0$) or did not decrease ($\Delta\text{HR} \geq 0$) following call playback.

Nestling Vocal Copy Similarity. To examine which combination of the five maternal in-nest call characteristics (average number of calls per female, number of elements per call, element rate, number of introductory notes, proportion of B elements) best explains the variation in vocal copy similarity, we used a model selection approach with all pos-

sible combinations of predictors to find the most parsimonious models. Copy accuracy (i.e., call similarity) was fitted as a Gaussian response in a GLMM. Population identity was included as random intercept to account for the nonindependence of the data, as this explained the variation in call similarity (calculated per nest) better than species identity (Akaike's information criterion corrected for sample size [AICc]; $\Delta\text{AICc} = -1.3$) and data limitations meant that they could not be included simultaneously. We accounted for incubation day by including it as a covariate in the analyses. All variables were transformed to z-scores before including them in the model. Calculating the variance inflation factors (VIFs) indicated very low collinearity among predictors (all $\text{VIF} < 1.64$; Zuur et al. 2010). To disentangle the within-population response from consistent differences among populations, we also ran models that, in addition to the main effect of each predictor, included the population mean. This mean predictor represented the difference in the within- and between-subject effect and should be nonsignificant if within- and between-population effects were effectively the same, whereas the main effect then represents the within-population response (van de Pol and Wright 2009). Model selection was based on AICc (Akaike 1973; Burnham and Anderson 2002), with models that are better supported by the data showing lower AICc values. We assessed the importance of in-nest call characteristics for explaining variation in copy similarity based on their estimated effect size and the marginal (proportion of total variance explained by the fixed effects) and conditional (proportion of total variance explained by both fixed and random effects) R^2 (Nakagawa et al. 2017). To test the robustness of our results in the presence of two female-offspring pairs with relatively low copy similarity (see "Results"), we performed sensitivity analyses by replacing these values with the cutoff values for outliers (i.e., $\text{quartile}_1 - 1.5 \times \text{interquartile range} = 0.42$; Tukey 1977). All statistical analyses were performed in R (ver. 4.0.5; R Core Team 2021) and packages lme4 (Bates et al. 2015), glmmTMB (Brooks et al. 2017), MuMIn (Barton 2020), Climwin (van de Pol et al. 2016), and ggbreak (Xu et al. 2021).

Results

Variation in In-Nest Calls

Four element types could be identified from the in-nest call recordings during incubation, and species varied in the number and type of these elements that they produced (fig. 1; tables 2, S3). Four species had calls with A and B elements (SFW, RBFW, VFW, TBGW); three species had calls with A, B, and C elements (SPLFW, WWFW, PCFW); and one species had calls with B, C, and D elements (RWWF; fig. 1; table S3). There were significant interspecific

Table 2: Order of element types per in-nest call during incubation, shown in four females per species

Species, nest ID	Track ID	Order of element types per call	Incubation call syntax
SFW:			
64.13	T001389	AABAAAB	2AB3AB
57.13	T000574	AAABAABAA	3AB2AB2A
C15.35	T000998	AAAABBBABAAAABAAAA	4A3B2AB4AB4A
UNB2012	T002365	BBBBBA	5BA
SPLFW:			
SPL35	T000537	ABBBBAABBBACA	A4B2A3BACA
SPL09	T000533	CBBBACBC	C3BACBC
SPL24	T000535	AABC	2ABC
SPL25	T000536	AABBCBCB	2A2BCBCB
RBFW:			
B13-138	T000249	BBBBBBA	6BA
B14-105	T000416	BBBBBA	5BA
B13-19	T000186	AABBBBBBBB	2A8B
D14-11	T000631	BBBBBB	6B
WWFW:			
T3	T000543	BBBBBB	6B
T18	T000544	BBBBCCCCAA	5B4C2A
T25	T000545	BAABBBBA	B2A3BA
T34	T000546	BBBAABBB	3B2A3B
RWFW:			
N8.2	T000565	DBBBBBCCCC	D5B4C
N8.1	T002026	DDDDBBCC	4D2B2C
N35.3	T000567	BBBBCCCCC	4B5C
N14.1	T002080	DBBBBBBBBBBBBBBBBBBB	D19B
VFW:			
BV14-101	T000553	BBBBAAAAAAAAAAAA	4B11A
BV14-113	T000554	BBAAAAAAAAAAAAAAAAAAAAAAAAAAAA	2B24A
BV13-47	T001988	BBBBBBAAAAAAAAAAAAAAAAAAAA	7B16A
BV14-55	T000551	BBBBBBBBBBBBAAAAAAAAAAAAAAAAAAAA	12B20A
PCFW:			
105b	T002610	AACCCCCCCCCCBB	2A11C2B
117b	T002613	AABACCCCCC	2ABA7C
110a	T002614	BCCCCCCCCCAABBBA	B10C2A3BA
107	T002617	BBBBBBB	7B
TBGW:			
T12	T002626	BAAABAAAAAA	B3AB6A
T25	T002628	ABBBBAA	A4B2A
T34	T002629	ABCAA	ABC2A
T50A	T002630	BBBBBBBBBBBB	12B

Note: The species abbreviation is shown for superb fairy wren (SFW), splendid fairy wren (SPLFW), red-backed fairy wren (RBFW), white-winged fairy wren (WWFW), red-winged fairy wren (RWFW), variegated fairy wren (VFW), purple-crowned fairy wren (PCFW), and thick-billed grass-wren (TBGW). For each call, we include the nest ID, track ID (the label name for the archived audio file), the order of element types per call, and the shorthand incubation call syntax to describe the element type order. The number of non-B elements before the first B element (introductory notes) is 1.1 ± 2.3 (mean $\pm$ SD).

differences in the number of maternal in-nest calls (fig. 3a; table S2), number of elements per call (fig. 3b; table S2), element rate (total number of elements per second; fig. 3c; table S2), and number of introductory notes (fig. 3d; table S2; GLM/GLMM: species: all $P < .001$). Interestingly, although across all species combined there was no evidence for collinearity in any of the in-nest call characteristics, the species with the lowest number of calls per hour (i.e., VFW) had the

highest number of elements per call and the fastest element rate (fig. 3).

Experiment: Element Type and Number of A Elements

SFW embryos responded to experimental call playback by reducing their HR (i.e., the orientation response; fig. 4a, 4b). Embryos decreased their HRs more in response to five

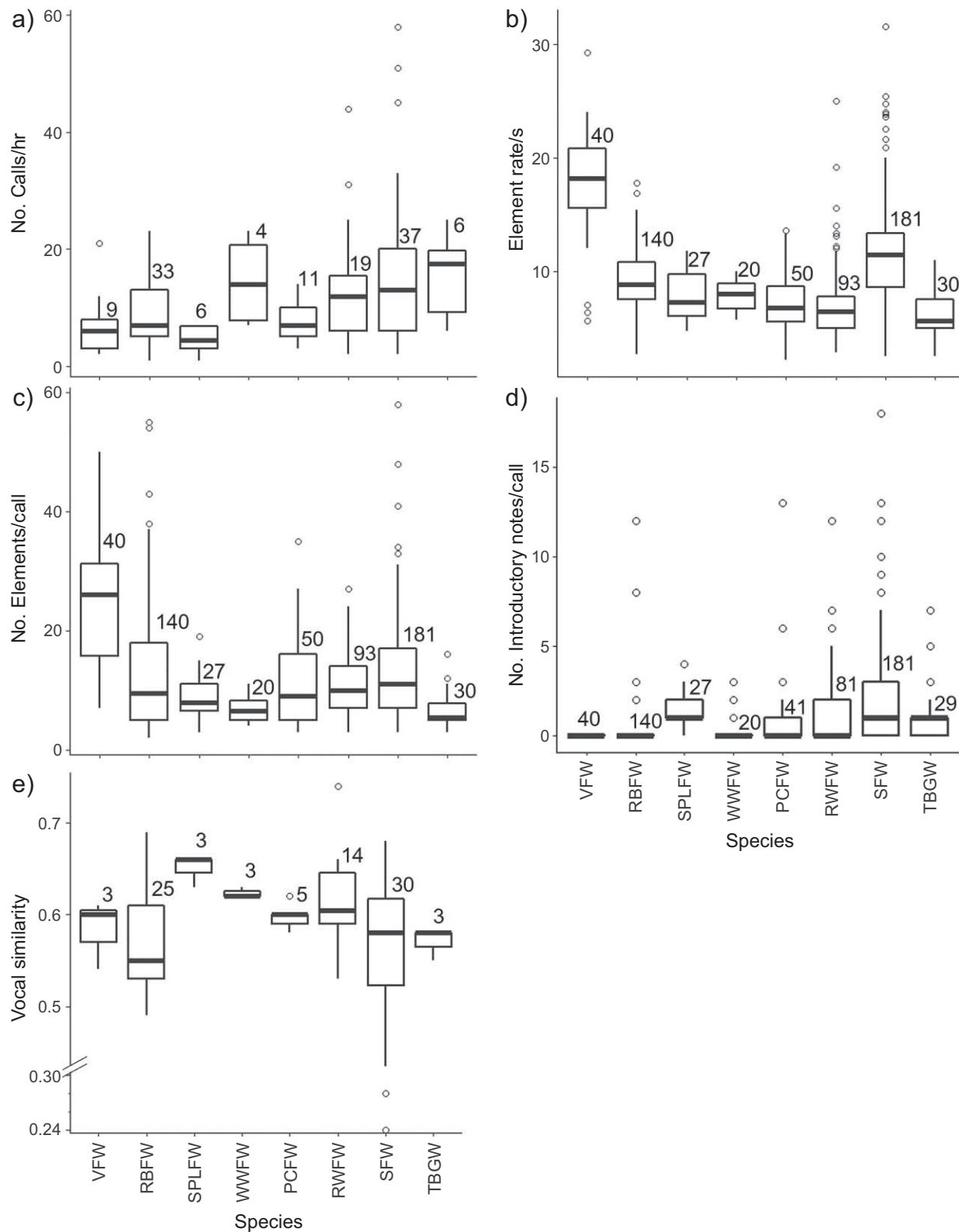


Figure 3: Boxplots showing the median, lower and upper quartile ranges of the number of in-nest calls per hour (a), number of elements per call (b), element rate (number of elements per second; c), number of non-B elements (introductory notes) before the first B element per call (d), and nestling vocal copy similarity of the B element in eight malurid species (e). Numbers next to each box indicate the sample sizes (i.e., number of females in a; number of calls in b, c, and d; and number of nestlings in e). VFW = variegated fairy wren; RBFW = red-backed fairy wren; SPLFW = splendid fairy wren; WWFW = white-winged fairy wren; PCFW = purple-crowned fairy wren; RFWF = red-winged fairy wren; SFW = superb fairy wren; TBGW = thick-billed grass-wren.

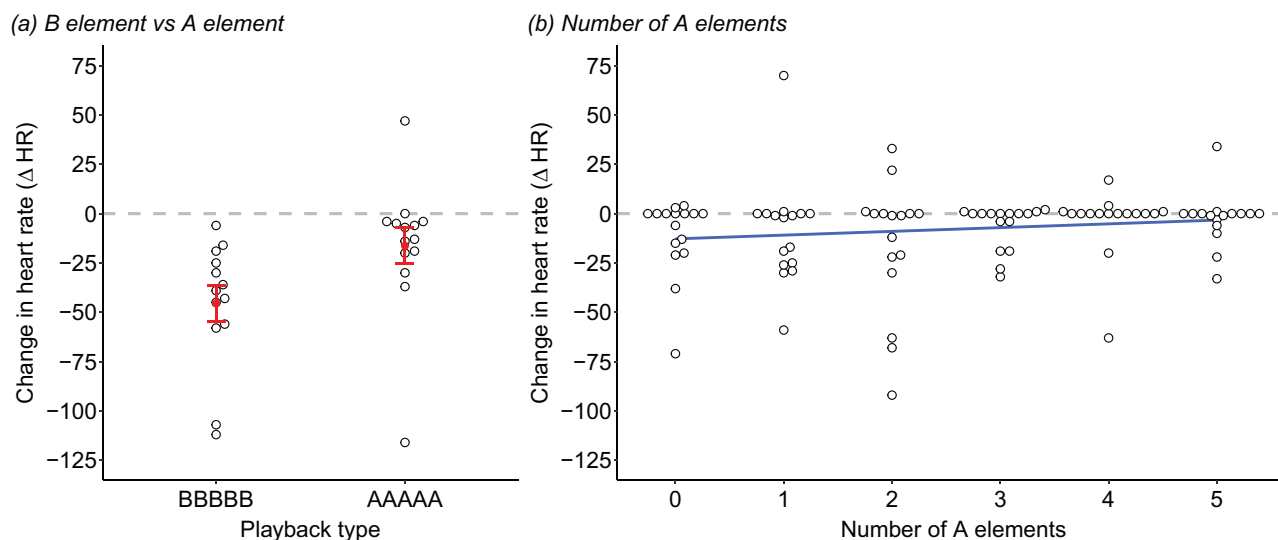


Figure 4: Change in heart rate (Δ HR, beats per minute) between baseline HR and HR in the second after call exposure in superb fairy wren embryos. *a*, Embryos showed a greater decrease in HR (generalized linear mixed model [GLMM]: $P = .004$) in response to five B elements (BBBBB) versus five A elements (AAAAA) in our 2014 experiments. Mean $\pm$ SE data with raw data overlaid. *b*, Number of A elements in a five-element call (0–5) did not significantly predict embryos' Δ HR following playback (GLMM: $P = .159$) in our 2022 experiments. 0 = BBBBB; 1 = ABBBB; 2 = AABBB; 3 = AAABB; 4 = AAAAB; 5 = AAAAA.

B elements (BBBBB) versus five A elements (AAAAA; $z = -2.85$, $P = .004$; fig. 4*a*; table S4). The number of A elements (range: 0–5) in a broadcast call did not statistically predict the strength of embryos' HR response ($z = 1.41$, $P = .159$; fig. 4*b*; table S5, pt. a). When we analyzed Δ HR as a binary response, calls with more A elements (and hence fewer B elements) showed a trend to be less likely to elicit decreases in embryo HR ($z = -1.81$, $P = .070$; table S5, pt. b).

Nestling Vocal Copy Similarity

The vocal similarity (copy accuracy) between the maternal B element (produced as part of the maternal in-nest call during incubation) and nestling B element (produced as a begging call after hatch) varied considerably both within and among species (fig. 3*e*; table S2). As we predicted, differences in copy similarity across species were best explained by variation in call tempo (element rate: $\beta = -0.25 \pm 0.11$ SE) and the number of introductory notes before the first B element ($\beta = -0.24 \pm 0.11$ SE; table S6, model 1). Specifically, copy similarity was higher when females called at a slower rate and used fewer introductory notes (fig. 5*a*, 5*b*). In contrast to our prediction, there was no evidence that call composition explained any additional variation in vocal copy similarity, because adding the total number of calls (table S6, model 2 vs. 1), number of elements per call (table S6, model 5 vs. 1), or the proportion of calls containing the B element (table S6, model 3 vs. 1) to the best-supported model increased rather than decreased AICc values. The results remained unchanged after adding

the population mean values (table S7), indicating that the reported associations were not due to consistent differences in any of these predictors among populations. The model support for the inclusion of element rate and number of introductory notes to explain variation in copy similarity was rather strong (cumulative model weights = 0.80 and 0.79, respectively) with a conditional (through random and fixed effects) variance of 20% and marginal variance of 14% of the variation in copy similarity accounted for in the best-supported model (table S6, model 1). Element rate and introductory notes explained similar amounts of variation in copy similarity ($R^2_{\text{element rate}} = 0.09$; table S6 model 7; $R^2_{\text{intro notes}} = 0.08$; table S6, model 8). However, closer inspection of the data revealed that the observed associations may be largely driven by two female-offspring pairs with relatively low copy similarity (fig. 5). A subsequent sensitivity analysis revealed that the association between copy similarity and element rate was robust to these two data points ($\beta_{\text{element rate}} = -0.23 \pm 0.11$ SE), but this was not the case for the association between copy similarity and number of introductory notes ($\beta_{\text{intro notes}} = -0.14 \pm 0.11$ SE). We also performed an outlier test using the testOutliers function from the DHARMA package, which shows that there are no more extreme values than expected by chance ($P = .15$).

Discussion

This study had three main aims: to describe and compare characteristics of in-nest calls during incubation in eight Maluridae species, to experimentally test the effect of element

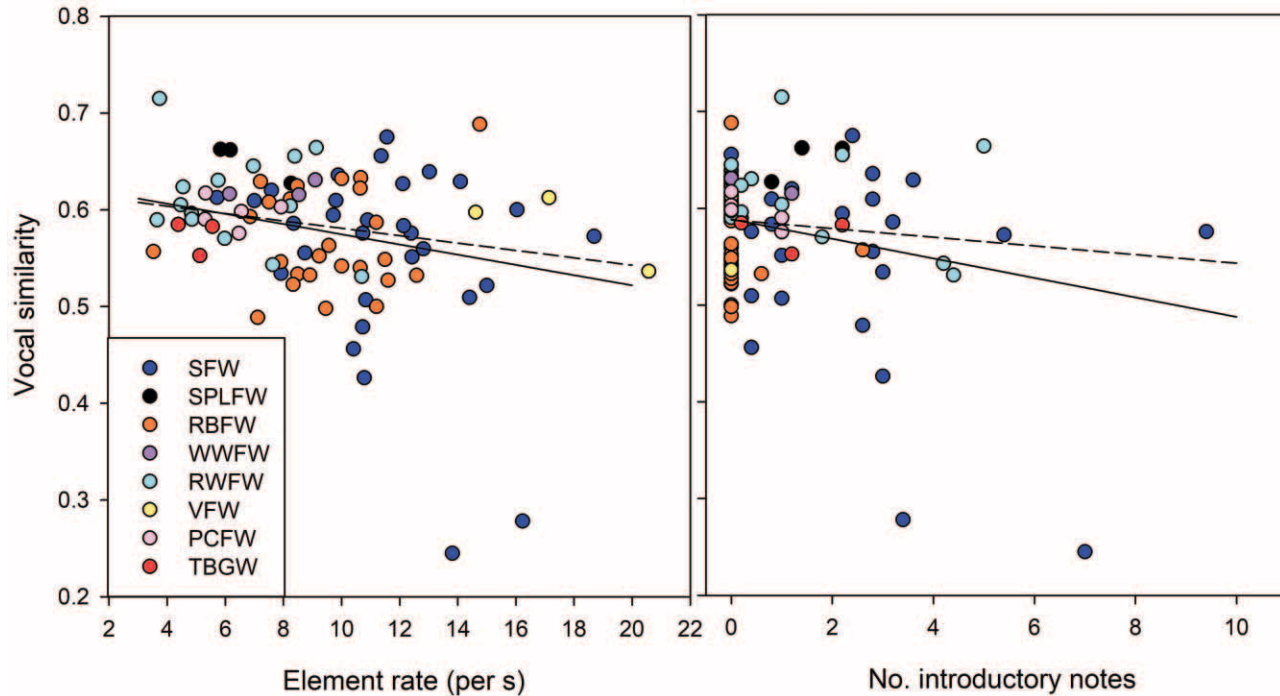


Figure 5: Relationship between vocal similarity of nestling begging calls to maternal in-nest call B element of 86 Maluridae females and element rate (a) and the number of non-B elements (introductory notes) before the first B element (b). Estimates for solid trend lines were derived from model 1 (table S6). Note that a sensitivity analysis shows that the association between vocal similarity and element rate is robust to two female-offspring pairs with very low vocal similarity (0.24 and 0.28, respectively), although this was not the case for the association between vocal similarity and the number of introductory notes (see “Results”). Dashed trend lines show the slopes from the sensitivity analyses. SFW = superb fairy wren; SPLFW = splendid fairy wren; RBFW = red-backed fairy wren; WWFW = white-winged fairy wren; RWFW = red-winged fairy wren; VFW = variegated fairy wren; PCFW = purple-crowned fairy wren; TBGW = thick-billed grass-wren.

type and elemental composition on an embryo’s response to a maternal call, and to examine which maternal call characteristics best predict nestling vocal copy similarity. All females in all species produced in-nest calls during incubation, providing evidence for the ubiquity of in-nest calling by malurid females. Across these eight species, we described four element types that comprise maternal in-nest calls. Intriguingly, all species produced a B element (defined as being structurally similar to their nestlings’ begging call), although sometimes (4% of calls) the B element was absent in one call of a particular female but present in another of her calls. The B element was present in the majority (96%) of maternal in-nest calls, whereas elements A, C, and D occurred in different combinations in different species. Maternal in-nest calling differed across species in every other parameter we measured, including the number of calls, number of elements per call, and element rate (or call tempo). Prenatal playback experiments showed that SFW embryos were more responsive to B elements (rather than A elements), which suggests enhanced attention to particular sounds and sound contexts during the embryonic stage (see also Colombelli-Négrel and Kleindorfer 2017).

Given that females from all eight malurid species produced in-nest calls, we suggest that in-nest calling behavior may be the ancestral state, at least in malurids (for adult female song, see also Odom et al. 2014), and that maternal vocalizations are likely to provide a large component of embryos’ prenatal sound stimulation. The importance of prenatal sound for imprinting and sensory development has been well documented in a small number of precocial, non-vocal-learning birds (e.g., Gottlieb 1971; Lickliter and Stoumbos 1991; Bolhuis and Van Kampen 1992) but has been largely unexplored in vocal-learning species (but see Colombelli-Négrel et al. 2021). Indeed, many classic studies on the mechanisms of song learning used subjects that were acoustically isolated as nestlings, under the assumption that prenatal sensory inputs would not alter vocal development (e.g., Marler 1970; Marler and Peters 1977; Price 1979). Nevertheless, evidence in SFWs indicates that vocal learning of maternal calls can begin in ovo (Colombelli-Négrel et al. 2012), and recent work in zebra finches suggests that prenatal exposure to parental “heat calls” influences a suite of physiological and behavioral traits (Mariette and Buchanan 2016; Katsis et al.

2021), including song production learning (Katsis et al. 2018). If in-nest calls are shown to be widespread across vocal learning taxa and to affect the sensory or vocal development of embryos, then interventions such as artificial incubation (e.g., of endangered species in captive-breeding programs) may inadvertently deprive offspring of important vocal stimulation during development.

A structural resemblance between maternal in-nest calls and nestling begging calls, consistent with prenatal vocal learning, has previously been shown in both SFWs and RBFWs (Colombelli-Négrel et al. 2012, 2016). In this study, malurid embryos copied their mother's B element more accurately if their mother's calls were slower (i.e., had a slower element rate). This correlational evidence supports the hypothesis that pupil-directed vocalizations, which are partly characterized by their slower tempo, may facilitate vocal learning by better capturing offspring attention (Chen et al. 2016). An extensive future playback experiment could explicitly test whether maternal call rate drives vocal copy similarity. The data provided here cannot rule out the possibility that genetic influences on maternal element rate and offspring imitation drive the observed correlation, and future cross-fostering studies will be important to rule this out. We also acknowledge that we cannot definitely make the claim that maternal calls are exclusively learned in ovo in RBFWs because we also detected in-nest calls by mothers after hatch in this species, although we analyzed only in-nest calls by mothers collected during the incubation phase in this study. Nonassociative sound learning in embryos has been shown to occur in ovo and was previously measured in RFWs and SFWs (Colombelli-Négrel et al. 2021). At the proximate level, maternal calling to embryos potentially shapes neural architecture (Rivera et al. 2019; Antonson et al. 2021), with possible consequences for sound learning and nestling begging call structure, and we may find these effects in all malurid species. From a phylogenetic perspective, prenatal vocal communication by mothers to their embryos could be the ancestral state in vocal learning species (Odom et al. 2014), which remains to be tested.

The adaptive value of prenatal vocal training, should it be occurring, could be multifaceted and include increased survival, for example, when vocal copy similarity is rewarded with food delivery to offspring (Colombelli-Négrel et al. 2016) or with parental rejection of brood parasitic cuckoos in the nest (Colombelli-Négrel et al. 2012). Another potential adaptive benefit of early-life vocal tutoring and sound learning could be increased reproductive success if birds with better vocal tutors and better prenatal sound learning have larger vocal repertoires as adults (Evans and Kleindorfer 2016; Kleindorfer et al. 2018) to defend a territory and/or attract a mate. We have previously experimentally shown that female SFWs increase their calling rate to embryos when the threat of brood parasites in the study area

increases (Kleindorfer et al. 2014a) and that high rates of in-nest calling increase nest predation risk (Kleindorfer et al. 2014b). Given the plasticity of female calling behavior in relation to prevailing ecological conditions and the high cost of pupil-directed calling behavior, we expect a range of fitness benefits and selection pathways shaping mother-offspring vocal ontogeny across species and systems.

As we predicted, SFW embryos responded more strongly to experimental playback of B elements than to A elements, highlighting the importance of the signature B element for parent-offspring communication. We also predicted that increasing the number of introductory (A) elements in a call would enhance an embryo's response by drawing its attention to the stimulus, as in zebra finches (Chen et al. 2016). This was not supported, however, as we found no significant relationship between the number of A elements and the strength of an embryo's playback response. We do not know how the proportion of A and B elements may affect HR, as the proportion of both elements changed concurrently for each playback. Despite a stronger embryonic response to B elements in SFWs, 54% (98/181) of maternal calls had introductory A elements. If the target of pupil-directed vocal learning is the maternal signature B element, later produced as the nestling begging call, then why do fairy wrens use multiple element types in their in-nest calls? Avian embryos across taxa show a habituation response to sound when repeatedly exposed to vocalizations from the same individual (Colombelli-Négrel et al. 2021). Hence, one plausible explanation for why mothers produce other element types in addition to the B element is to reduce the risk of habituation to the B element. Future research should assess this more directly by testing whether embryos habituate more weakly to repeated broadcast of B elements when they are preceded by A elements.

In addition to reducing the risk of habituation during the embryo stage, mothers may produce two or more element types if such behavior is useful as a latent cause of reinforcement learning after hatching. According to this idea, offspring first learn an order association between two sound elements (e.g., A and B elements) that is later used as a memory building block for structure learning (about contingencies, grammar or syntax, and other expectations). For example, after eggs hatch we have observed that female SFWs arriving at the nest with food produce a feeding call that structurally resembles the maternal in-nest A element (S. Kleindorfer and D. Colombelli-Négrel, unpublished data) and that nestlings respond with a begging call that resembles their mother's in-nest B element (Colombelli-Négrel et al. 2012). These observations generate a new and testable hypothesis about latent cause influences on structure learning. During the embryo stage, females may train a learned association in embryos by exposing them to two different element types per call, allowing offspring

to establish an association between these two element types. After hatching, mothers may produce the A element when arriving at the nest with food, and nestlings are rewarded with food when they respond with the B element. The benefit of producing at least two element types during the embryo stage to reduce the risk of habituation can be modified by mothers in a novel context after hatch, so their offspring acquire additional cognitive skills. We fully acknowledge that such a call-and-response scenario remains to be tested but could align with the latent cause model of structure learning. Latent cause variables (a variable that is a hidden cause of an expressed and temporally separate behavior) can lead to structure learning when the hidden variables are rewarded and reinforced in a new context (Courville et al. 2003, 2004; Gershman et al. 2015).

In conclusion, there was a consistent pattern of temporal onset of maternally guided vocalization behavior, which occurred during the embryo phase in eight malurid species. Females in all eight malurid species produced in-nest calls with a B element during incubation, but the non-B elements differed across species. As the species occupy habitats with vastly different rainfall patterns, nesting density, and social group size (Brouwer et al. 2017; Odom et al. 2021) and call and song elements may be acquired by processes of innovation and cultural evolution, such variation across species in element types may not be surprising. We also report on hypothesis-driven support for pupil-directed vocalization behavior. When mothers produced in-nest calls containing B elements that had slow element rate, the offspring produced a B element (begging call) with higher vocal copy similarity. Future research could explore whether species differ in the association between in-nest call characteristics and offspring vocal learning, potentially revealing selection pathways for different learning mechanisms across socioecological contexts. Our experimental study in SFWs showed that embryos are more responsive to calls comprising B elements rather than A elements, raising questions about why mothers produce non-B elements. This finding opens the pathway to explore parental vocal tutoring in the context of habituation-avoidance tactics and latent cause models to understand the ontogeny of cognitive processes. Perhaps early memory formation guided, for example, by mothers calling to their embryos, creates opportunity for vocal tutors to deconstruct the memory components at a later life stage and thereby guide structure learning and expectancy violation, with potential consequences for social and vocal learning across life stages (Epstein 1961; Hannon and Johnson 2005).

Acknowledgments

We thank the Department for Environment and Water (DEW) for approval to conduct the research in South

Australia. We also thank Cleland Wildlife Park for access to the park; Adrian and Julia Wayne and other staff of the Department of Biodiversity, Conservation and Attractions (DBCA) Science division in Manjimup; staff at the Australian Wildlife Conservancy Mornington Wildlife Sanctuary; and Karen and Michael Keely for logistical support and hospitality. We extend special thanks to all of the field assistants and volunteers who assisted with fieldwork, especially Christine Evans, Sara Criddle, Jenelle Dowling, Petra Hanke, Chelsey Hunts, Teresa Iglesias, Katharina Mahr, Serena Mathew, Ingrid Stirnemann, Kyle Sutherland, Amy Slender, and Valeria Zanollo. The present study complied with institutional, national, and international ethical guidelines. The study was approved by the Animal Welfare Committee of Flinders University (E325-404) and adhered to a DEW scientific permit to conduct the research (Z24699). The Western Australian Department of DBCA and the Australian National University Animal Experimentation Committee licensed the field research on red-winged fairy wrens. The field research on purple-crowned fairy wrens was approved by the Monash University Animal Ethics Committee (BSCI/2015/11), Western Australian Department of Environment and Conservation (U 29/2015-2018; BB003816), and the Australian Wildlife Conservancy. We thank the Australian Research Council (ARC; DP190102894 and DP150103595), the Hermon Slade Foundation, the Australian Geographic Society, the National Geographic Society, the Australian Acoustical Society, the Holsworth Wildlife Research Endowment from the Ecological Society of Australia, and the Nature Foundation and Birds SA for financial support to S.K. and D.C.-N. L.B. was funded by an ARC Discovery Early Career Research Award (DE130100174), and A.P. was funded by an ARC Future Fellowship (FT110100505). The authors declare no conflict of interest.

Statement of Authorship

S.K., M.E.H., and D.C.-N. designed the research, and S.K. wrote the first draft of the manuscript; S.K., L.B., N.T., A.P., M.L., A.C.K., L.K.C., V.I.A., and D.C.-N. collected the data; D.C.-N. performed all acoustic analyses; L.B., F.J.S., A.C.K., and S.K. statistically analyzed the data; all authors developed the ideas presented in the article, including edits and final approval.

Data and Code Availability

The data for this article have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.f1vhhmh0p>; Kleindorfer 2023).

APPENDIX

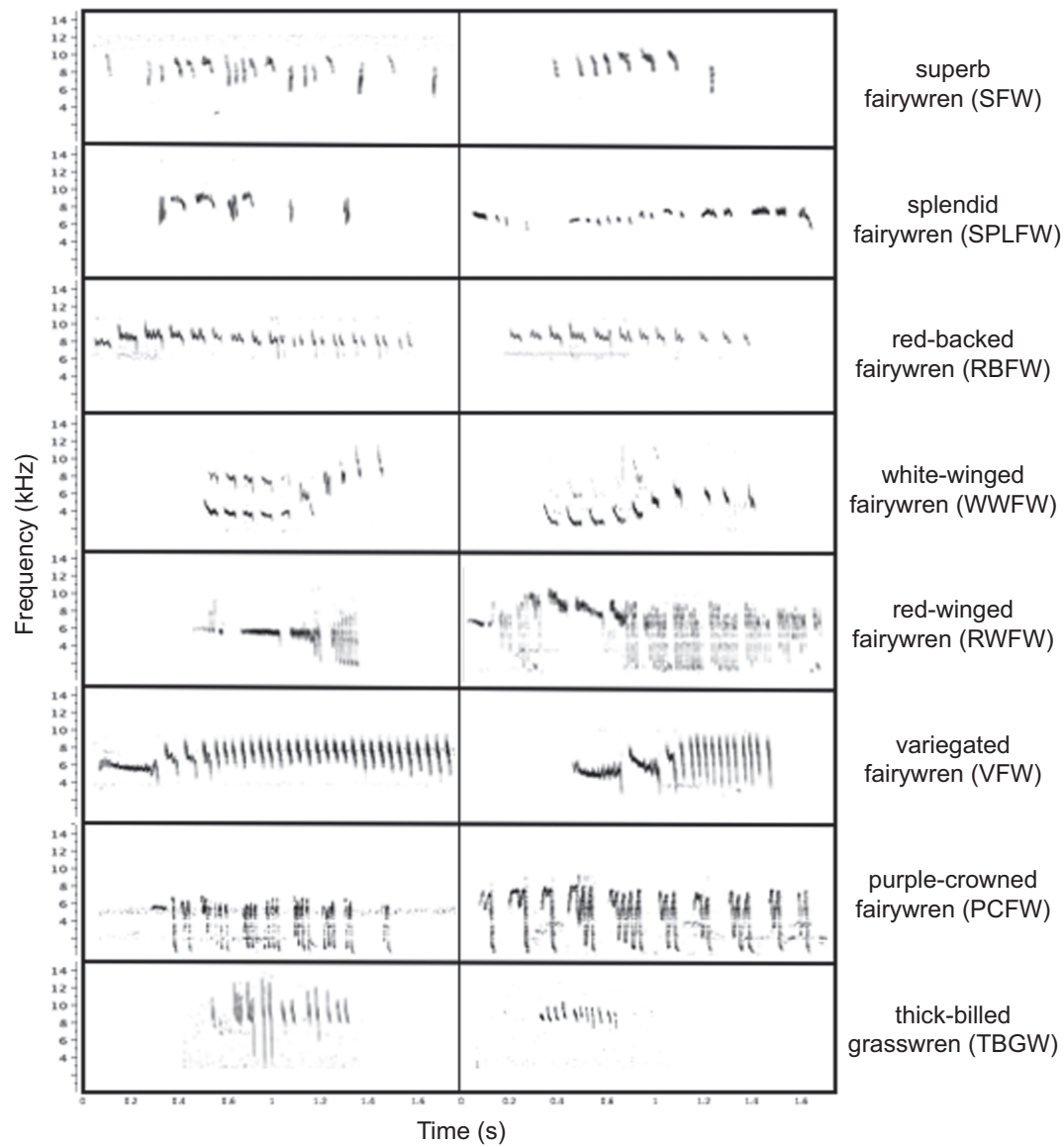


Figure A1: Examples of in-nest calls produced by Maluridae females during incubation. Each panel shows the call of one female, with two examples per species from eight species. The species differ in the number and type of elements (A–D) per in-nest call, although all species produce a B element. Details on the acoustic characteristics for each element type are shown in table 1, and examples of each element type are shown in figure 1.

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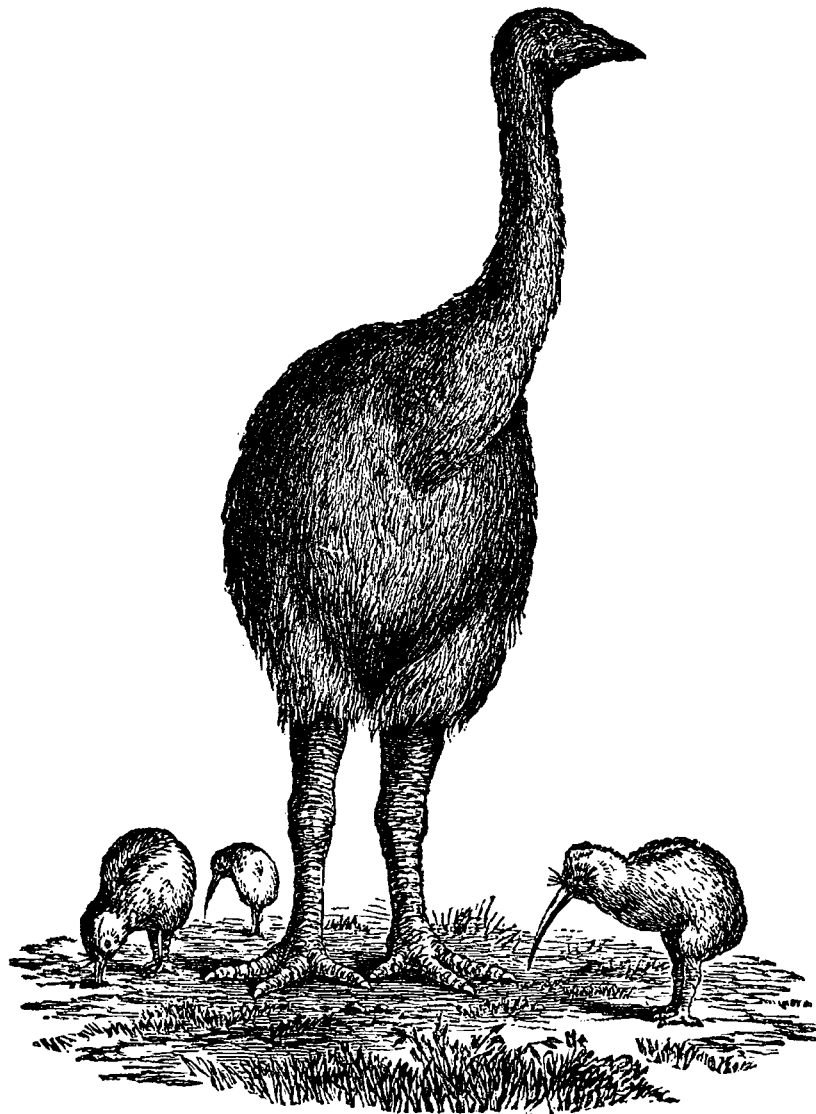
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Associate Editor: Kate L. Laskowski
Editor: Erol Akçay



“The true wingless birds of New Zealand, however, are the kiwis, of which four species are known; all of these totally incapable of flight, being, as their scientific name (*Apteryx*) implies, without wings; they have, however, the merest rudiments of wings, that can be felt underneath the feathers.” Figured: “*Apteryx* and *Dinornis* of New Zealand.” From “The Giant Birds of New Zealand” by I. C. Russell (*The American Naturalist*, 1877, 11:11–21).