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RESEARCH ARTICLE

Vocal imitation of mother's calls by begging Red-backed Fairywren nestlings increases parental provisioning

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ABSTRACT

Prenatal imitative learning is an emerging research area in both human and non-human animals. Previous studies in Superb Fairywrens (*Malurus cyaneus*) showed that mothers are vocal tutors to their embryos and that better imitation of maternal calls yields more parental provisions after hatching. To begin to test if such adaptive behavior is widespread amongst Australasian wrens in Maluridae, we investigated maternal in-nest calling patterns in Red-backed Fairywrens (*Malurus melanocephalus*). We first compared the structure of maternal and nestling call elements. Next, we examined how in-nest calling behavior varied with parental behaviors and ecological contexts (i.e. prevalence of brood parasitism and nest predation). All Red-backed Fairywren females called to their eggs during incubation and they continued to do so for several days after hatching at a lower rate. Embryos that received more calls per hour during the incubation period (but not the nestling period) developed into hatchlings with higher call element similarity between mother and young. Female call rate was mostly independent of nest predation but in years with more interspecific brood parasitism, nestling element similarity was greater and female call rates tended to be higher. Playback experiments showed that broods with higher element similarity to their mother received more successful feeds. The potential for prenatal tutoring and imitative begging calls in 2 related fairywren taxa sets the stage for a full-scale comparative analysis of the evolution and function of these behaviors across Maluridae and in other vocal-learning lineages.

Keywords: imitation, oscine, vocal tutor, parental investment

La imitación vocal de los llamados maternos por polluelos de *Malurus melanocephalus* incrementa el aprovisionamiento parental

RESUMEN

El comportamiento de imitación prenatal es un área de investigación emergente en animales humanos y no humanos. Estudios previos en *Malurus cyaneus* demostraron que las madres son tutores vocales de sus embriones y que una mejor imitación de los llamados maternos provoca mayor abastecimiento parental luego de la eclosión. Para empezar a determinar si este comportamiento adaptativo se distribuye ampliamente entre los Maluridae de Australasia investigamos los patrones de llamados maternos en los nidos en *Malurus melanocephalus*. Primero comparamos la estructura de los elementos del llamado entre polluelos y madres. Luego examinamos cómo el comportamiento de llamado en los nidos variaba con el comportamiento parental y el contexto ecológico (i.e. la prevalencia del parasitismo de cría y la depredación de los nidos). Todas las hembras de *M. melanocephalus* emitieron llamados para sus huevos durante la incubación y continuaron haciéndolo a una tasa más baja por varios días luego de la eclosión. Los embriones que recibieron más llamados por hora durante el periodo de incubación (pero no durante el periodo de anidación) se desarrollaron en polluelos con mayor similitud en los elementos del llamado entre madres e hijos. La tasa de llamados de las hembras fue independiente de la depredación de los nidos, pero en años con mayor parasitismo de cría la similitud en los elementos del llamado fue mayor y la tasa de llamado de las hembras tendió a ser mayor. Experimentos de reproducción de sonidos previamente grabados demostraron que las nidadas con mayor similitud en elementos del llamado con los de su madre recibieron más viajes de alimentación exitosos. Tras encontrar que la enseñanza prenatal y los llamados de ruego por alimentación que imitan los llamados de la madre están presentes en dos taxones de Maluridae cercanamente relacionados, se justifica un análisis comparativo a gran escala de la evolución y función de estos comportamientos en Maluridae y en otros linajes con aprendizaje vocal.

Palabras clave: imitación, inversión parental, maestro vocal, oscino

INTRODUCTION

Vocal learning in songbirds, in which young need to learn their species-specific vocalizations from adult tutors during a sensitive period (e.g., Konishi 1965, Rose et al. 2004), offers many selective advantages. It allows individuals to signal local genetic adaptation (Nottebohm 1969), increase their mating success (by indicating increased quality for example: Nowicki et al. 1998, Brumm et al. 2009, Lachlan and Nowicki 2012), and enhance social interactions (Payne 1982, Berg et al. 2011) and kin recognition (Treisman 1978, Sharp et al. 2005) (reviewed in Nowicki and Searcy 2014). However, most prior studies focused on the advantages of such behavior at the adult stage, with few studies investigating the potential benefits of vocal learning earlier in life (but see Colombelli-Négrel et al. 2012, Kleindorfer et al. 2014a, Shizuka 2014).

To date, prenatal vocal learning was only demonstrated in humans (e.g., Kisilevsky et al. 2009, Moon et al. 2013) and one songbird species, the Australian Superb Fairywren (*Malurus cyaneus*) (Colombelli-Négrel et al. 2012, 2014; Kleindorfer et al. 2014b). In our long-term research, we found that Superb Fairywren females called to their eggs and vocally tutored their embryos a particular element of their incubation call during incubation, which was later produced by the nestlings as a begging call (Colombelli-Négrel et al. 2012). Better-imitated maternal call elements by nestlings elicited more food provisioning from parents and revealed the presence of foreign chicks, including interspecific brood parasite nestlings that did not learn as embryos (Langmore et al. 2008, Colombelli-Négrel et al. 2012). Females with higher incubation call rate produced offspring with higher begging call similarity and females increased their incubation call rate when there were more parasitic Horsfield's Bronze-cuckoos (*Chalcites basalis*) in the area (Colombelli-Négrel et al. 2012, Kleindorfer et al. 2014b). However, female Superb Fairywrens needed to trade off the benefits of incubation calling with potential costs because higher maternal incubation call rates at the nest resulted in increased egg predation (Kleindorfer et al. 2014a).

The evidence for Superb Fairywren incubation call tutoring and embryonic learning led us to question how ecologically and taxonomically widespread this behavior might be (Colombelli-Négrel et al. 2012, 2014). Is it unique to a single population of a single host species parasitized by a particular species of call-mimetic cuckoos (Ranjard et al. 2010), or is it widespread in songbirds where maternal incubation call production induces learning by embryos to produce imitative begging calls? Brood parasites and their hosts are good model systems to address the functions and constraints of learning (e.g., Hauber et al. 2001, Colombelli-Négrel et al. 2012, Kleindorfer et al. 2014a,b), because there are strong selection pressures on host birds to learn

to discriminate against nests with brood parasites (e.g., Davies 2000, Feeney and Langmore 2013, Kleindorfer et al. 2013a, Moskat et al. 2014). Therefore, we begin to answer these questions by assessing whether females of the Red-backed Fairywren (*M. melanocephalus*), a close relative of the Superb Fairywren (Driskell et al. 2011), also call to their embryos, and if the resulting hatchlings produce elements of their mother's calls.

Here, we examine in-nest calling behaviors of females and young in relation to parental behaviors and 2 fitness-relevant ecological contexts (brood parasitism prevalence and nest predation). We address these questions in order to test the hypothesis that in-nest vocalizations during incubation are a female adaptation that balances the potential benefits of tutoring (e.g., recognition of own young) with the potential costs (e.g., increased nest predation), as found in Superb Fairywrens. First, we ask, do female Red-backed Fairywrens call to their young during incubation? Given that this is a close phylogenetic relative of the Superb Fairywren (Driskell et al. 2011) and a host of brood parasitic cuckoos (Rowley and Russell 1997, Langmore 2013), we predict that females will also call to their embryos. Second, does female call rate during incubation covary positively with call element similarity between mother and nestlings? We predict higher element similarity in nests with higher call rate during incubation (Colombelli-Négrel et al. 2012, Kleindorfer et al. 2014b). Third, is parental food provisioning higher at nests with higher call element similarity? We test this by broadcasting conspecific nestling begging calls at non-parasitized nests. We predict less feeding by parent birds to the broadcast of begging calls with lower element similarity (Colombelli-Négrel et al. 2012). Fourth, do females increase their call rate during incubation when brood parasitism is more prevalent? We predict lower call rates in years with lower cuckoo prevalence (Kleindorfer et al. 2014b). Finally, and fifth, is nest predation positively related to call rates during incubation? Based on the work in Superb Fairywren, we predict higher egg predation at nests with higher call rates (Kleindorfer et al. 2014a).

METHODS

Study Sites and Species

To examine female calling behavior, we recorded in-nest vocalizations from 67 Red-backed Fairywren nests, across 3 different study populations, and over 4 breeding seasons (September–January) during the years 2010, 2011, 2012, and 2013. We broadcast nestling begging calls at nests in 2012 and 2013 to test food provisioning by attending females in relation to element similarity. The 3 study sites were all in Queensland (Australia) with one site near Brisbane and 2 sites near Cairns: (1) Samsonvale Cemetery (27°16'S, 152°51'E), 38 km NE of Brisbane (2012–2013);

(2) Moomin (17°22'S, 145°25'E) and (3) Herberton (17°26'S, 145°22'E), both approximately 105 km SE of Cairns (2010–2013). These sites are hereafter referred to as Brisbane site (Samsonvale Cemetery) and Cairns sites (Moomin and Herberton).

Like most fairywren species in the Maluridae family (Cockburn 1998, 2006; Margraf and Cockburn 2013), Red-backed Fairywrens have a cooperative breeding system: young males may remain in their natal territory and provide “help” to their parents at the nest (Varian-Ramos et al. 2010). Similar to members of the genus (Mulder et al. 1994, Webster et al. 2004, Colombelli-Négrel et al. 2009), extra-pair paternity rates are high, with approximately half or more of the young being sired by extra-pair males (Webster et al. 2008). At our study sites, breeding starts at the beginning of the rainy season (around September–October) and continues until February (Karubian et al. 2009, Webster et al. 2010). Females build the nest and incubate the eggs alone, but all members of the group feed the young (see Varian-Ramos et al. 2010). In these study populations, clutch size ranged between 2 and 4 eggs. Eggs hatched after ~13 days of incubation, and chicks fledged after ~12 days in the nest. In Maluridae, annual nest predation ranges from 0% to 83% (Rowley and Russell 1997, Colombelli-Négrel and Kleindorfer 2009). Red-backed Fairywrens are a primary host to Horsfield's Bronze-cuckoos, and a secondary host to Brush Cuckoos (*Cacomantis variolosus*) (Rowley and Russell 1997, Langmore 2013).

Do Female Red-backed Fairywrens Call to Their Eggs?

We recorded in-nest vocalizations during incubation from all Red-backed Fairywren nests (27 nests at the Brisbane site, 40 nests at the Cairns sites) for 2 continuous hours per nest between days 10 and 14 of incubation. We also recorded nestling begging calls at 36 of the 67 nests (10 at the Brisbane site, 26 at the Cairns sites) for 2 continuous hours per nest between days 3 and 7 of the nestling phase. Eleven of those 36 nests (3 at the Brisbane site, 8 at the Cairns sites) were also recorded daily from hatching.

We recorded all vocalizations produced at the nest using either (1) an Olympus linear LS-10 PCM recorder (Olympus, Tokyo, Japan), (2) a Wildlife Acoustics Song Meter SM2 Autonomous recording unit (Wildlife Acoustics Inc., Concord, Massachusetts, USA), both with a sample rate of 24 KHz in 16 bit PCM format, or (3) a Zoom Handy Recorder H4n (Zoom Corporation, Ronkonkoma, New York, USA) at sample rate of 44.1kHz in 16 bit. All recorders had integrated stereo microphones and were placed directly under the nest as close as possible without causing disturbance (usually 20–30 cm). All recordings were done in the morning between 0500 and 1100 hours locally. We transferred all the recordings onto an Apple MacPro (Apple Corporation, Cupertino, California, USA)

to visualize them with Amadeus Pro 1.5 (HairerSoft, Kenilworth, UK) and Raven Pro 1.4 (Bioacoustics Research Program 2011). Spectrograms of audio recordings were created using the Hann algorithm (16-bit sample format; discrete Fourier transform, DFT = 512 samples; frequency resolution = 190 Hz; time resolution = 7.57 ms; frame overlap = 50%).

Do the Chicks Imitate the Elements in Their Mother's Calls?

To compare our results with results found in Superb Fairywrens, we followed methods used in Colombelli-Négrel et al. (2012). Specifically, for each nest with recordings of nestling calls, we selected 5 begging elements from the nestling begging calls. All elements were randomly selected using Raven Pro 1.4 based on the fact that there was no overlapping sound. We used 5 begging elements from 5 different begging sequences to ensure independence of the data. To test if begging call structure differed significantly across nests, we compared spectrograms between nestling begging call elements with spectrographic cross-correlation (SPCC) using batch correlation in Raven Pro 1.4 (see also Ranjard et al. 2010). To account for potential biases due to background noise between the different locations, we conducted the spectrographic cross-correlation analysis with a band pass filter between 2 kHz and 16 kHz. We then applied principal coordinate analysis (PCoA) using R-package software for Multivariate and Spatial analysis version 4 (Casgrain and Legendre 2001) to create 5 similarity values (PCoA coordinate values) per call comparison and an average similarity value (Cortopassi and Bradbury 2000, Baker and Logue 2003). PCoA produces a set of orthogonal axes of the distance or dissimilarities between objects in the ordination space (Legendre and Legendre 1998). Each axis has an eigenvalue whose magnitude indicates the amount of variation captured in that axis and the first 5 eigenvalues explain most of the variation in the data set (Baker and Logue 2003). Therefore, objects ordinated closer to one another are more similar than those ordinated further away. The first 5 eigenvalues represent our 5 similarity values per call, which we then averaged to create the average similarity value. For more details on the methods see Colombelli-Négrel et al. (2012).

Female in-nest calls contained 2 element types, referred to in this study as call elements A and B (Figure 1). In this study, we focused on element B for 2 reasons: (1) because of its preliminary structural resemblance with the nestling begging call element in this study and the other fairywren species (Colombelli-Négrel et al. 2012) and (2) because previous research on Superb Fairywrens showed that spectrogram cross-correlation analysis of whole incubation calls and of element B only showed the same statistical results when testing for individual differences between

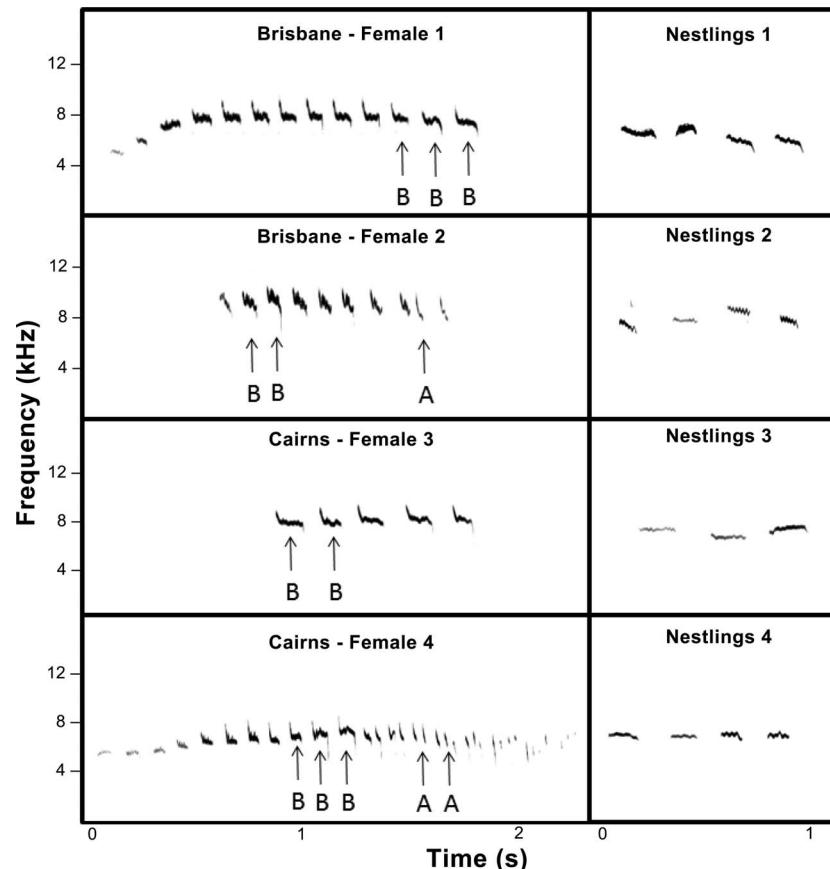


FIGURE 1. Spectrograms from 4 nests (2 from the Brisbane site and 2 from the Cairns sites) showing some examples of the 2 element types described in this study: element A and element B; element B is also referred to as the signature element.

females (Colombelli-Négrel et al. 2012). For all recorded nests, we selected a random sample within element B of 5 elements for each female. Element B selection was based on the pattern that there was no overlapping sound and all 5 elements were selected from 5 different begging sequences to ensure independence of the data as described above for begging elements. To test whether element B structure differed significantly between females, we compared spectrograms between female element B using spectrographic cross-correlation and principal coordinate analyses as described above.

To specifically test whether chicks imitate the element B in their mother's calls, we calculated the structural similarity between spectrograms of nestling's begging call element and their mother's element B (element similarity) using spectrographic cross-correlation and principal coordinate analyses as described above. For each recording made during the incubation phase, we noted the number of in-nest calls produced per hour by females during the incubation period to calculate average call rate. We then analyzed the relationship between female in-nest call rate

during incubation and element similarity between mother element B and nestling begging call element.

Do Females Adjust Their Food Provisioning in Relation to Element Similarity?

To test whether female Red-backed Fairywrens provide more food to young with higher element similarity (i.e. chicks with begging call elements structurally more similar to element B of the attending female), we conducted playbacks of conspecific nestling begging calls at 9 non-parasitized nests (4 at the Brisbane site, 5 at the Cairns sites) in 2012 and 2013. All the tested nests had only one female and one male feeding the nestlings. However, males were only present for 48% of the playback experiments, and therefore, we focused on female responses only.

For each nest, we broadcast nestling begging calls that were recorded at a Red-backed Fairywren nest other than our focal nest; the begging calls used were recorded at 5 other Red-backed Fairywren nests in our study sites. We matched to the day (in days post-hatch) the age of the recorded nestling used in the experiment with the age of

the nestlings in the tested focal nest. All playbacks were made of 4 nestling begging call elements to control for difference in female response due to variation in begging call rate or intensity. All playbacks were normalized at -15 dB and saved as uncompressed 16 bit 44.1 kHz WAV files using Amadeus Pro 1.5. We calculated element similarity between 5 elements B from the attending female in the focal nest and 5 experimental nestling begging call elements. As above, for “natural element similarity,” we used spectrographic cross-correlation and principal coordinate analyses. Each nest was only tested once and we did not know element similarity scores at the time of the experiment.

The 9 playback experiments using nestling begging calls were done at 9 nests during morning feeding (between 0500 and 1000 hours); each nest had 2–4 nestlings that were 4–7 days old. An observer hid in vegetation 10 m from the nest, and each time an adult was at the nest, the observer broadcast a selected stimulus for 5 s using either (1) a battery-powered amplified speaker placed under the nest and controlled by the observer via a Bluetooth connection to an Apple iPod (Apple Corporation, Cupertino, California, USA) or (2) a RadioShack amplified speaker (Catalog No. 277-1008C; RadioShack, Fort Worth, Texas, USA) connected to an Apple iPod Nano via a 20 m cable. The RadioShack speaker has been used in other published playback experiments successfully without distortion (see Hauber et al. 2001, Uy et al. 2009, Benedict 2010, Oh and Shaw 2013). In addition, the use of the 2 speakers was balanced in terms of which track was used with which speaker (with 50% of the trials in the low similarity range and 50% in the high similarity range) and so any difference in responses observed would not have resulted from differences in speaker quality. Each experiment lasted for a total of 30 minutes. We audio-recorded the experiments using either (1) a Zoom Handy Recorder H4n, (2) an Olympus linear LS-10 handheld PCM recorder, or (3) a Marantz PMD661 recorder (recording at 98 kHz and 24 bit PCM; Marantz, Kanagawa, Japan) with a Sennheiser ME67 microphone (Sennheiser, Hanover, Germany). We noted the percentage of visits that led to successful feeds from the female (when a female at nest rim inserted her beak into nestlings' gape and left without the food in her beak) in response to the playback (Colombelli-Négrel and Kleindorfer 2010, Colombelli-Négrel et al. 2012). An unsuccessful visit was defined as a visit where the female approached the nest with food in its bill but left without feeding the nestlings (i.e. left with the food still in its bill). We always waited until we saw one successful feed to start the experiment to rule out effects of human presence on the lack of feeding and to confirm that the presence of the equipment itself would not prevent the adults from attending the nest.

What are the Ecological Contexts of Female In-nest Calling?

To identify potential ecological contexts of tutoring and learning in Red-backed Fairywrens, we examined female in-nest calling behavior in relation to brood parasite prevalence and nest predation. We used data collected at 654 nests (359 at the Brisbane site and 295 at the Cairns sites) between 2010 and 2013 and related these data to cuckoo prevalence and egg predation in our study sites. We only obtained in-nest recordings for 67 of those 654 nests but all 654 nests were used to estimate parasitism prevalence and predation rates. Nests were categorized as parasitized if a cuckoo egg or a cuckoo nestling was found in the nest. Across years, brood parasite prevalence was either below 1.45% (range: 0–1.45%) or above 3% (range: 3–9%; see Results). Therefore, we categorized cuckoo prevalence for our study years as either lower (brood parasite prevalence $<1.5\%$) or higher (brood parasite prevalence $>3\%$). To test if high female in-nest call rate may function to reveal intruder cuckoo nestlings, we compared female call rate and cuckoo prevalence (lower, higher) between years.

We also investigated whether high female call rate during incubation increased egg predation. We considered nests as depredated during the egg stage if evidence of predation was present (nest torn or disheveled) or the eggs were missing from the nest between visits. Out of the 654 monitored nests, we have data on both female in-nest call rates during incubation and egg predation at 28 nests.

Statistical Analyses

We used SPSS 18.0 for Windows (SPSS, Chicago, Illinois, USA) for all statistical analyses. Data are shown as mean \pm S.E. The Kolmogorov–Smirnov test showed that all percentage data complied with the conditions of normality. To test for individual characteristics in mother and nestling calls, we analyzed the first 5 similarity values and the average similarity (independent variables) produced by the PCoA analysis in 3 MANOVAs, with either individual (for female element B) or nest (for nestling begging call elements and for the comparison between female and nestling calls) as between-subject factor. We used a paired *t*-test to compare female in-nest call rate per hour during the incubation and nestling periods at the same nests. We used 2 linear regression analyses (weighted by site) to analyze the relationship between female in-nest call rate and element similarity between maternal element B and nestling begging call element during (a) the incubation period and (b) the nestling period. We used quadratic regression analysis to determine whether females varied their food provisioning in relation to element similarity in playback experiments. For our examination of the ecological contexts of in-nest call rate, we first transformed the average similarity score and the female

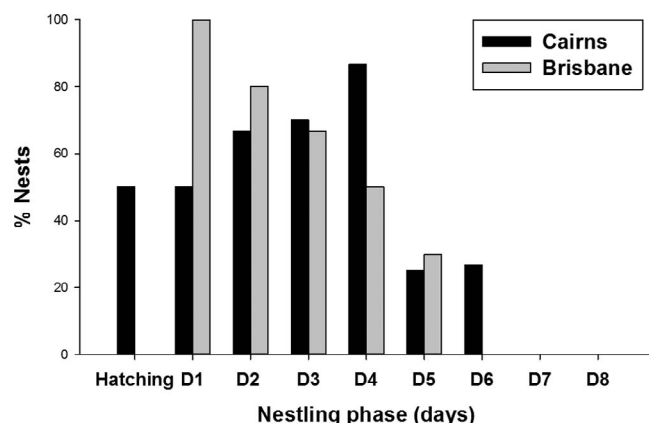


FIGURE 2. Percentage of nests at which incubation and post-hatching calls were detected after the onset of hatching: data are presented separately for Brisbane (in grey) and Cairns (in black).

call rate to satisfy the Shapiro–Wilk test ($P > 0.05$) for normality. We then used MANOVA to test for the interaction effect of cuckoo prevalence (lower, higher) and study sites (Brisbane, Cairns) on female call rate and average element similarity scores. To explore the interaction effect “cuckoo prevalence * site,” we statistically compared call rate and element similarity in relation to cuckoo prevalence (low, high) in each study site using an independent t -test. We used a binary logistic regression to test if predation outcome (survived, depredated) was predicted by the number of female in-nest calls per hour during incubation. Finally, we used an ANOVA and an independent t -test to test for the interaction effect of cuckoo risk, predation risk and study sites on female in-nest call rate.

RESULTS

Do Female Red-backed Fairywrens Call to Their Eggs?

All females monitored at all 67 nests (27 nests at the Brisbane site and 40 nests at the Cairns sites) produced in-nest calls when alone and incubating, and 62% of the females (70% at the Brisbane site and 59% at the Cairns sites) continued to call until day 5–6 of the nestling phase (Figure 2). This in-nest vocalization is hereafter referred to as “incubation and post-hatching call.” At the Brisbane site, the incubation and post-hatching call rate was 8.3 ± 1.2 calls per hour during incubation and 2.6 ± 0.5 calls per hour during the nestling period. At the Cairns sites, call rate was 9.6 ± 0.7 calls per hour during incubation and 3.0 ± 0.6 calls per hour during the nestling period. Call rate per hour was significantly lower during the nestling period (paired t -test: $t = 4.83$, $df = 20$, $P < 0.001$).

Do the Chicks Imitate the Elements in Their Mother’s Calls?

We recorded a total of 619 incubation and post-hatching calls from 27 females at the Brisbane site and 1,040 incubation and post-hatching calls from 40 females at the Cairns sites. We obtained recordings of both the female and her nestlings at 10 nests (267 begging events recorded in total) at the Brisbane site and at 26 nests (968 begging events) at the Cairns sites. Red-backed Fairywren nestlings used a single, repeated begging call element when begging for food (mean = 11.1 ± 2.5 begging events per hour at the Brisbane site; mean = 18.8 ± 3.5 begging events per hour at the Cairns sites). We found that begging call element structure differed significantly between nests for 4 of the 5 element similarity scores at the Brisbane site (Table 1A) and for all 5 similarity scores at the Cairns sites (Table 1B, Figure 3). Spectrogram cross-correlation analysis showed that the element B of each female was significantly different from the element B of any other female at both sites (Table 1, Figure 3).

When comparing the mother’s element B and her nestlings’ begging call element, we found that mother and offspring elements were significantly more similar than expected by chance for 3 of the 5 element similarity scores at the Brisbane site (Table 1A) and 4 of the 5 element similarity scores at the Cairns sites (Table 1B, Figure 3). We found that element similarity between female (element B) and nestling (begging call element) was positively related to the number of female incubation and post-hatching calls produced per hour during incubation (linear regression weighted by site: $\beta = 0.34$, $P = 0.05$, $n = 33$; Figure 4) but not during the nestling period ($\beta = -0.19$, $P = 0.42$, $n = 20$).

Do Females Adjust Their Food Provisioning in Relation to Element Similarity?

We experimentally tested whether female Red-backed Fairywrens increased their food provisioning at nests with higher element similarity (between the female element B and the nestling begging call element) at $n = 9$ nests with Red-backed Fairywren nestlings. We found that nestlings were fed more successfully when element similarity was higher (quadratic regression: $R^2 = 0.93$, $F = 38.64$, $df = 2$ and 6, $P < 0.0001$; Figure 5).

What are the Ecological Contexts of Female In-nest Calling?

Out of the 654 monitored nests, a total of 40 nests (6%) had evidence of parasitism (22 at the Brisbane site and 18 at the Cairns sites). The 2 populations differed in cuckoo parasitism prevalence: at the Brisbane site, 1–9% of the nests across years had evidence of cuckoo parasitism (Brush and Horsfield’s Bronze-cuckoos) while only 0–3% of the nests at the Cairns sites had evidence of cuckoo

TABLE 1. Results of spectrographic cross-correlation and principal coordinates analyses (PCoA) at the Brisbane site (1A) and at the Cairns sites (1B). For each site, we calculated 5 element similarity scores (ESS) as the structural similarity between (1) all female elements B, (2) all nestling begging call elements, and (3) mother element B and nestling begging call elements. The female elements B were recorded between days 10 and 12 of incubation and the begging calls 3–7 days after hatching. The data are presented for 27 nests at the Brisbane site and 40 nests at the Cairns sites.

Element similarity scores		df	F	P	Eta ²
(1A) Brisbane site					
(1) Similarity between female elements B (<i>n</i> = 27 females)	ESS 1	26	3.98	<0.0001	1.00
	ESS 2	26	4.77	<0.0001	1.00
	ESS 3	26	1.92	0.01	0.99
	ESS 4	26	2.87	<0.0001	1.00
	ESS 5	26	2.05	<0.01	0.99
	Av	26	3.73	<0.0001	1.00
(2) Similarity between nestling begging call elements (<i>n</i> = 10 nests)	ESS 1	9	6.04	<0.0001	1.00
	ESS 2	9	0.39	0.93	0.17
	ESS 3	9	4.89	<0.0001	1.00
	ESS 4	9	2.74	0.01	0.90
	ESS 5	9	2.70	0.01	0.90
	Av	9	2.73	0.01	0.90
(3) Similarity between Female elements B and nestling call elements (<i>n</i> = 10 nests)	ESS 1	9	2.25	0.04	0.83
	ESS 2	9	10.09	<0.0001	1.00
	ESS 3	9	5.05	<0.0001	1.00
	ESS 4	9	1.67	0.13	0.67
	ESS 5	9	1.71	0.12	0.69
	Av	9	4.97	<0.0001	1.00
(1B) Cairns sites					
(1) Similarity between female elements B (<i>n</i> = 40 females)	ESS 1	39	4.10	<0.0001	1.00
	ESS 2	39	2.07	<0.01	1.00
	ESS 3	39	2.61	<0.0001	1.00
	ESS 4	39	1.64	0.02	0.99
	ESS 5	39	1.72	0.01	1.00
	Av	39	3.10	<0.0001	1.00
(2) Similarity between nestling begging call elements (<i>n</i> = 26 nests)	ESS 1	25	4.39	<0.0001	1.00
	ESS 2	25	2.64	<0.0001	1.00
	ESS 3	25	1.88	0.01	0.98
	ESS 4	25	3.00	<0.0001	1.00
	ESS 5	25	2.17	<0.01	0.99
	Av	25	2.43	0.001	1.00
(3) Similarity between Female elements B and nestling call elements (<i>n</i> = 26 nests)	ESS 1	25	3.95	<0.0001	1.00
	ESS 2	25	3.38	<0.0001	1.00
	ESS 3	25	2.51	<0.01	1.00
	ESS 4	25	1.80	0.02	0.98
	ESS 5	25	1.46	0.10	0.93
	Av	25	4.20	<0.0001	1.00

parasitism (Horsfield's Bronze-cuckoo; see also Langmore 2013). Horsfield's Bronze-cuckoo nestlings were never abandoned at the Cairns sites (*n* = 6 parasitized nests) while they were abandoned in 46% of the cases at the Brisbane site (*n* = 13 parasitized nests).

We investigated whether females increased their in-nest call rate during the incubation and post-hatching period and whether nestlings had higher element similarity with their mothers when risk of brood parasitism was higher (cuckoo prevalence was categorized based on observed cuckoo parasitism during egg and nestling phase). We found a nonsignificant interaction effect of "cuckoo prevalence * site" on female call rate (MANOVA: $F = 3.25$, $df = 1$ and 35, $P = 0.081$) and a significant interaction

effect of "cuckoo prevalence * site" on nestling element similarity ($F = 4.82$, $df = 1$ and 35, $P = 0.033$). We also report the main effects for the MANOVA for "cuckoo risk" (call rate: $F = 1.93$, $df = 1$ and 35, $P = 0.174$; element similarity: $F = 4.94$, $df = 1$ and 35, $P = 0.033$) and "study site" (call rate: $F = 3.97$, $df = 1$ and 35, $P = 0.055$; element similarity: $F = 2.45$, $df = 1$ and 35, $P = 0.127$). To explore the interaction effect "cuckoo prevalence * site," we statistically compared call rate and element similarity in relation to cuckoo risk (low, high) in each study site separately. At the Brisbane site, female call rate did not differ in relation to years with high or low cuckoo prevalence (*t*-test: $t = 1.35$, $P = 0.19$) but element similarity was higher in years with higher cuckoo prevalence ($t =$

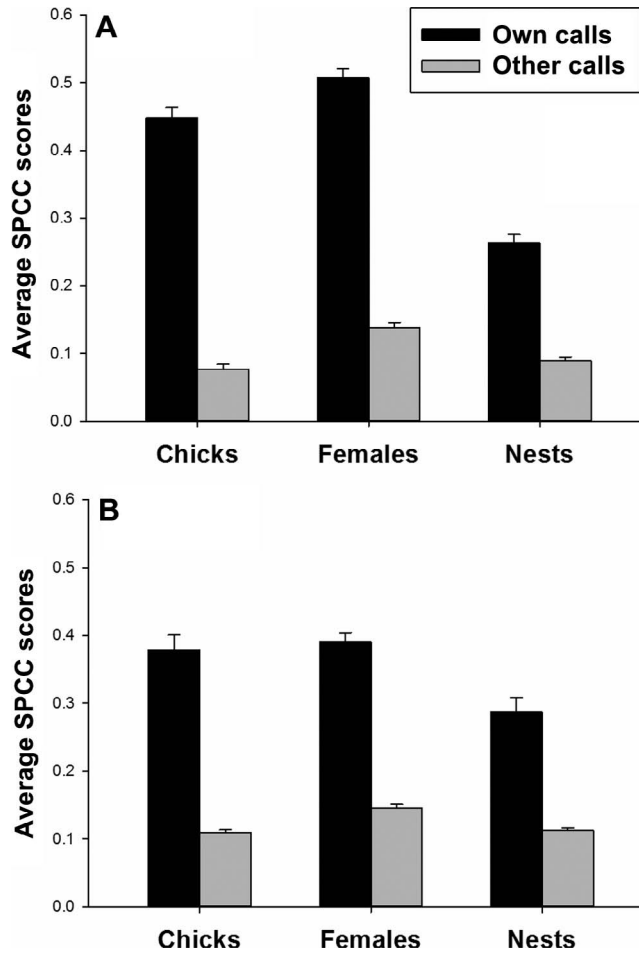


FIGURE 3. Average SPCC values (mean \pm SE) for (1) within vs. between female element B comparison, (2) within vs. between chick calls comparison, and (3) females vs. their own and other young element B comparison. The data are presented for (a) Brisbane ($n = 27$) and (b) Cairns ($n = 40$).

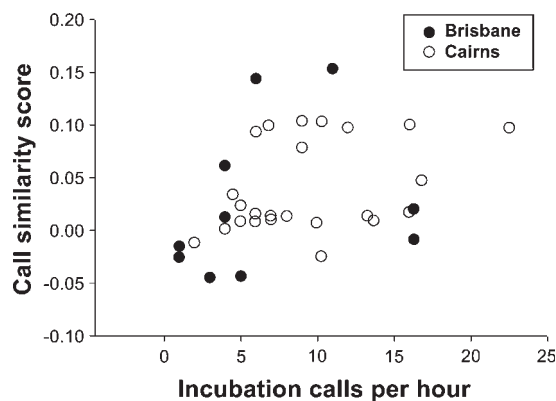


FIGURE 4. A positive correlation between incubation call rate and call similarity (regression weighted by site: $\beta = 0.34$, $p = 0.05$, $n = 33$).

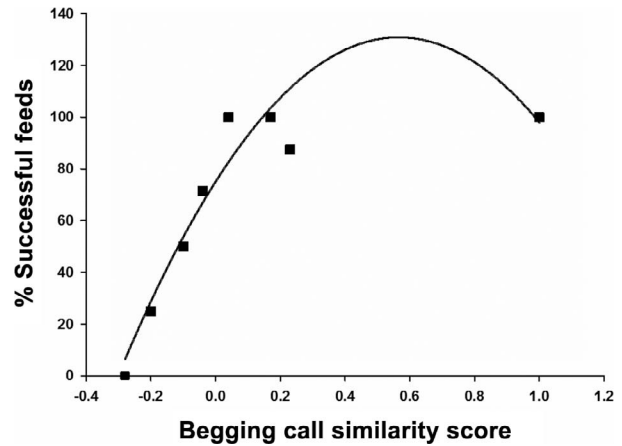


FIGURE 5. Percentage of nest visits that resulted in food delivery to nestlings (% successful feeds) in relation to call element similarity between the attending female's element B and the experimental nestling begging calls: we found that nestlings were fed significantly more when nestling element similarity was higher (quadratic regression: $R^2 = 0.93$, $F_{2,6} = 38.64$, $P < 0.0001$, $n = 9$).

-2.99 , $P = 0.02$) (Figure 6). At the Cairns sites, there was no statistically significant difference in either call rate or element similarity in relation to cuckoo prevalence (call rate: $t = -0.86$, $P = 0.41$; element similarity: $t = 0.005$, $P = 1.00$) (Figure 6).

The percentage of nests depredated during the incubation phase varied between 18% and 25% across our study years at the Brisbane site and between 6% and 19% at the Cairns sites. We found no statistical effect of call rate on

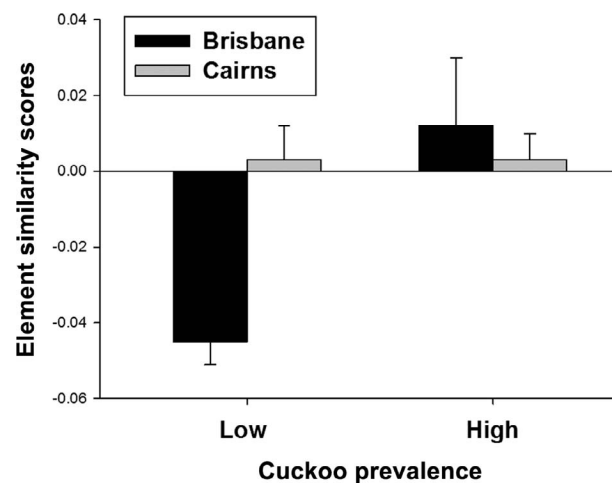


FIGURE 6. Nestling begging call element similarity in relation to cuckoo prevalence, defined as either lower (number of nests with evidence of parasitism $< 1.5\%$) or higher (number of nests with evidence of parasitism $> 3\%$). We found that element similarity between mother and young was higher when parasitism prevalence was higher ($F_{1,35} = 4.82$, $p = 0.03$) at the Brisbane site, but not at the Cairns sites. Bars depict mean \pm SE.

TABLE 2. Summary of the prenatal teaching and learning variables for Red-backed Fairywren (2010–2013) and Superb Fairywren (2007–2013): the table presents the number of nests recorded, the prevalence and timing of incubation calls, as well as the ecological context of incubation calls (brood parasite prevalence, nest predation).

	Red-backed Fairywren (Queensland)	Superb Fairywren (South Australia)
Nests with recording of incubation vocalizations	67	43
Prevalence of nests with incubation calls	100%	100%
Unique female signature element per nest	Yes	Yes
Unique begging call per nest	Partial	Yes
Cessation of incubation calls	~Day 5 post-hatching	Hatching Day
Incubation calls/hour (mean ± SE)	8.9 ± 0.9	12.9 ± 1.2
Incubation calls/hour (range)	4–28	4–41
Incubation call rate predicts begging call copy accuracy	Yes	Yes
Cuckoo parasitism prevalence (range)	0–9%	0–43%
Cuckoo prevalence predicts incubation call rate	Positive Trend	Positively
Predation percentage (range)	18–25%	34–83%
Incubation call rate increases egg predation	No	Yes

egg predation ($\beta = -0.03$, $df = 1$, $P = 0.71$). We explored call rate in relation to cuckoo prevalence (low, high), egg predation (survived, depredated), and study site (Brisbane, Cairns) using ANOVA. The three-way interaction effect “cuckoo prevalence * egg predation * study site” was not significant ($F = 2.28$, $df = 1$ and 61 , $P = 0.14$); the two-way interaction effects “cuckoo prevalence * study site” ($F = 1.21$, $df = 1$ and 61 , $P = 0.28$) and “egg predation * study site” ($F = 0.10$, $df = 1$ and 61 , $P = 0.75$) were also not significant nor were any main effects significant (all $P > 0.2$). The two-way interaction effect “cuckoo prevalence * egg predation” ($F = 6.21$, $df = 1$ and 61 , $P = 0.02$) was significant. When there were many cuckoos present, nest predation was lower when there was low call rate ($t = 2.11$, $P = 0.04$, $n = 36$). When there were few cuckoos present, call rate did not differ in relation to nest predation ($t = -1.01$, $P = 0.32$, $n = 26$).

DISCUSSION

Our findings provide an additional species-level example of in-nest calling during incubation in the Maluridae family. Red-backed Fairywren eggs that received more calls per hour during the later stages of incubation developed into hatchlings with higher element similarity scores between the nestling begging call element and their mother’s element B. In addition, at nests where playbacks with higher element similarity scores were broadcast, broods received more successful feeds from attending females, suggesting a potential fitness benefit of imitative calls in this species as previously found in Superb Fairywrens (Colombelli-Négrel et al. 2012). Regarding the ecological context of incubation calling behavior, we found relatively no impact of egg predation on call rates during incubation but females tended to increase their call rate (though nonsignificantly) and

broods showed consistently more element similarity during years of high cuckoo prevalence at the Brisbane site (but not at the Cairns sites). Such evidence for female incubation calling and imitative begging calls in 2 related fairywren taxa sets the stage for a full scale comparative analysis of the ecology and evolution of these behaviors across species.

Similarly to Superb Fairywrens (Colombelli-Négrel et al. 2012, 2014), Red-backed Fairywren females call to their young a particular element of their incubation and post-hatching call (element B), which is later produced by the nestlings as part of their begging calls. The positive correlation between female call rate during incubation and element similarity (between mother and young) suggests a possible role of learning, as previously shown in Superb Fairywrens using both observational and cross-fostering approaches (Colombelli-Négrel et al. 2012). However, without cross-fostering approaches, we cannot fully exclude that nestlings have more similar calls to their mother’s calls because of shared genes or epigenetics. It is also possible that embryos that heard more calls during the incubation period were more stimulated during their development and consequently developed into nestlings better skilled in call production or capable of producing their mother’s element B with greater precision. In addition, one striking difference in incubation call behavior between Red-backed and Superb Fairywrens is the timing of the calls (see Table 2 for comparison of the 2 species). Superb Fairywren females stopped calling as soon as the eggs hatched (Colombelli-Négrel et al. 2012), while ~70% of Red-backed Fairywren females continued to call after hatching (until day 5 post hatching). Therefore, Red-backed Fairywren hatchlings also had the opportunity to hear their mother’s calls as nestlings and the possibility that they also could learn the element after hatching in this species cannot be

completely excluded. Future studies should use cross-fostering experiments or rear nestlings in acoustic isolation to rule out the possibility of a genetic contribution and identify the potential sensitive periods in the ontogeny of vocal learning in Red-backed Fairywren young.

We examined 2 fitness-critical ecological contexts of incubation calling (cuckoo parasitism prevalence and egg predation). While our results only showed nonsignificant trends, this study suggests a potential brood parasitism context of incubation calling in the Red-backed Fairywren, as found in the Superb Fairywren (Colombelli-Négrel et al. 2012, Kleindorfer et al. 2014b). Specifically, we found that call rate during incubation tended to be higher in years of high cuckoo prevalence, but only at the Brisbane site. Such difference between sites may be explained by the fact that females at the Brisbane site experienced higher parasitism rates than at the Cairns sites (1–9% of the nests at the Brisbane site had evidence of cuckoo parasitism compared to only 0–3% of the nests at the Cairns sites). It should also be noted that brood parasite prevalence was much lower in Red-backed Fairywrens than in Superb Fairywrens (Table 2), which might explain why we mostly found nonsignificant trends. The highest reported brood parasite prevalence in Red-backed Fairywrens was 9% within a given year (Langmore 2013; M. S. Webster personal observation) while brood parasite prevalence in Superb Fairywrens can be as high as 43% per year (Langmore et al. 2003, 2009; Colombelli-Négrel et al. 2012; Kleindorfer et al. 2014b) (Table 2).

Contrary to the study on Superb Fairywrens (which used an experimental approach and found a significant positive effect of high incubation call rate on egg predation; Kleindorfer et al. 2014a), we found only partial support for a predation cost to incubation calling in the Red-backed Fairywren. Conversely, it should be noted that predation rates were much lower in the Red-backed Fairywrens (18–25% of nests depredated) than in the Superb Fairywrens (34–83% of nests depredated, Table 2), which may explain why we did not detect any observational effect of call rate on egg predation in this species. Playback experiments following those of Kleindorfer et al. (2014a) would be needed to assess the causal impact of incubation calling on egg predation and vice versa.

Playback experiments showed that nests with higher element similarity scores received more successful feeds from attending females. This pattern was comparable to that in Superb Fairywrens, where parental nest visitation was higher when we broadcast offspring calls versus conspecific or cuckoo calls (although we did not examine call similarity directly) (Colombelli-Négrel et al. 2012). However, in this study, there was no effect of similarity once similarity was 0.0 or greater, suggesting that females may simply classify calls as “similar” vs “non-similar” to

make their feeding decisions. This is again analogous to patterns found in Superb Fairywrens, where adults did not respond to cuckoo call playback specifically but instead reacted to conspecific calls the same way they did to cuckoo calls and thus discriminated between “own” vs “other” calls (Colombelli-Négrel et al. 2012). Therefore, females would only avoid feeding when calls were very dissimilar but would feed any nestling that produced reasonably similar calls. Such a hypothesis is supported by playback experiments showing that cuckoo calls that were similar to those of the Red-backed Fairywren nestlings present in the nest elicited normal feeding (D. Colombelli-Négrel personal observation).

The differences in the ecological contexts of incubation calling between Red-backed Fairywren populations as well as between Red-backed Fairywren and Superb Fairywren species (Table 2) raise new ideas into the possible function(s) of incubation calling. Given that male and female Superb Fairywrens adjust parental care across nestling and fledgling phases in relation to perceived predation risk (Colombelli-Négrel et al. 2010a,b), and adjust their behavioral response to brood parasite risk using only acoustical cues (Kleindorfer et al. 2013a), it is highly plausible that fairywrens use acoustical signals of their offspring for other parental investment decisions. We suggest that if higher element similarity between mother and young is the consequence of superior development during the embryonic stage, then females could use element similarity as a signal to invest in nestlings of higher quality (Haig 1990). Similarly, if females in better condition were able to call more and provision their nestlings at a greater rate, they may also produce offspring that could expend more resources on brain areas associated with vocal learning (e.g., Nowicki et al. 2002, Spencer et al. 2003, Liu et al. 2015). This again would lead to greater element similarity and could serve as a signal for mothers to invest in higher-quality offspring. In addition, if Red-backed Fairywren young start to learn their calls at the embryonic level, females could also use element similarity as a learning outcome and invest in young that are good learners. In vocal learning species such as the fairywren species—where young learn their song from a tutor (e.g., Rose et al. 2004, Greig et al. 2012)—individuals with better learning capacity would have higher vocal complexity as adults (see Buchanan et al. 2003, 2013) and thus could attract more mates and/or have more chances of establishing themselves within a territory (e.g., Payne 1982, Woodgate et al. 2012). There is growing evidence that vocal complexity in fairywrens shows geographically distinct patterns in both males and females (Greig and Webster 2013, Kleindorfer et al. 2013b). While these potential dialectic patterns seem to have an early ontogenetic origin in other dialect singing taxa (Shizuka 2014), such

an ontogenetic origin has not yet been examined in relation to prenatal environment in fairywrens.

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Author information: Diane Colombelli-Négrel developed and designed the methods, analyzed the data, and wrote the paper; Michael S. Webster contributed substantial resources, supervised the experiments, and provided critical comment on draft manuscripts; Jenéle L. Dowling performed the experiments and provided critical comment on draft manuscripts; Mark E. Hauber substantially edited the paper and helped develop the methods; and Sonia Kleindorfer conceived the idea, supervised the research, and substantially edited the paper.

LITERATURE CITED

- Baker, M. C., and D. M. Logue (2003). Population differentiation in a complex bird sound: A comparison of three bioacoustical analysis procedures. *Ethology* 109:223–242.
- Benedict, L. (2010). California Towhee vocal duets are multifunctional signals for multiple receivers. *Behaviour* 147:953–978.
- Berg, K. S., S. Delgado, K. A. Cortopassi, S. R. Beissinger, and J. W. Bradbury (2011). Vertical transmission of learned signatures in a wild parrot. *Proceedings of the Royal Society of London, Series B* 279:585–591.
- Bioacoustics Research Program (2011). Raven Pro: Interactive Sound Analysis Software. Version 1.4. Cornell Lab of Ornithology, Ithaca, NY, USA.
- Brumm, H., S. A. Zollinger, and P. J. Slater (2009). Developmental stress affects song learning but not song complexity and vocal amplitude in Zebra Finches. *Behavioral Ecology and Sociobiology* 63:1387–1395.
- Buchanan, K. L., K. Spencer, A. Goldsmith, and C. Catchpole (2003). Song as an honest signal of past developmental stress in the European Starling (*Sturnus vulgaris*). *Proceedings of the Royal Society of London, Series B* 270:1149–1156.
- Buchanan, K. L., J. L. Grindstaff, and V. V. Pravosudov (2013). Condition dependence, developmental plasticity, and cognition: Implications for ecology and evolution. *Trends in Ecology & Evolution* 28:290–296.
- Casgrain, P., and P. Legendre (2001). The R Package for multivariate and spatial analysis, version 4.0 d6 User's Manual. Département de sciences biologiques, Université de Montréal, Québec, Canada.
- Cockburn, A. (1998). Evolution of helping behavior in cooperatively breeding birds. *Annual Review of Ecology, Evolution, and Systematics* 29:141–177.
- Cockburn, A. (2006). Prevalence of different modes of parental care in birds. *Proceedings of the Royal Society of London, Series B* 273:1375–1383.
- Colombelli-Négrel, D., M. E. Hauber, and S. Kleindorfer (2014). Prenatal learning in an Australian songbird: Habituation and individual discrimination in Superb Fairy-wren embryos. *Proceedings of the Royal Society of London, Series B* 281:20141154.
- Colombelli-Négrel, D., M. E. Hauber, J. Robertson, F. J. Sulloway, H. Hoi, M. Griggio, and S. Kleindorfer (2012). Embryonic learning of vocal passwords in Superb Fairy-wrens reveals intruder cuckoo nestlings. *Current Biology* 22:2155–2160.
- Colombelli-Négrel, D., and S. Kleindorfer (2009). Nest height, nest concealment, and predator type predict nest predation in Superb Fairy-wrens (*Malurus cyaneus*). *Ecological Research* 24:921–928.
- Colombelli-Négrel, D., and S. Kleindorfer (2010). Video nest monitoring reveals male coloration-dependent nest predation and sex differences in prey size delivery in a bird under high sexual selection. *Journal of Ornithology* 151:507–512.
- Colombelli-Négrel, D., J. Robertson, and S. Kleindorfer (2010a). Nestling presence affects the anti-predator response of adult Superb Fairy-wrens (*Malurus cyaneus*). *Acta Ethologica* 13:69–74.
- Colombelli-Négrel, D., J. Robertson, F. J. Sulloway, and S. Kleindorfer (2010b). Extended parental care of fledglings: Parent birds adjust anti-predator response according to predator type and distance. *Behaviour* 147:853–870.
- Colombelli-Négrel, D., B. E. Schlotfeldt, and S. Kleindorfer (2009). High levels of extra-pair paternity in Superb Fairy-wrens in South Australia despite low frequency of auxiliary males. *Emu* 109:300–304.
- Cortopassi, K. A., and J. W. Bradbury (2000). The comparison of harmonically rich sounds using spectrographic cross-correlation and principal coordinates analysis. *Bioacoustics* 11:89–127.
- Davies, N. B. (2000). Cuckoos, Cowbirds and Other Cheats. T and AD Poyser, London, UK.
- Driskell, A. C., J. A. Norman, S. Pruett-Jones, E. Mangall, S. Sonsthagen, and L. Christidis (2011). A multigene phylogeny examining evolutionary and ecological relationships in the Australo-papuan wrens of the subfamily Malurinae (Aves). *Molecular Phylogenetics and Evolution* 60:480–485.
- Feeney, W. E., and N. E. Langmore (2013). Social learning of a brood parasite by its host. *Biology Letters* 9:20130443.
- Greig, E. I., B. N. Taft, and S. Pruett-Jones (2012). Sons learn songs from their social fathers in a cooperatively breeding bird. *Proceedings of the Royal Society of London, Series B* 279:3154–3160.

- Greig, E. I., and M. S. Webster (2013). Spatial decoupling of song and plumage generates novel phenotypes between 2 avian subspecies. *Behavioral Ecology* 24:1004–1013.
- Haig, D. (1990). Brood reduction and optimal parental investment when offspring differ in quality. *The American Naturalist* 136:550–556.
- Hauber, M. E., S. A. Russo, and P. W. Sherman (2001). A password for species recognition in a brood-parasitic bird. *Proceedings of the Royal Society of London, Series B* 268:1041–1048.
- Karubian, J., J. P. Swaddle, C. W. Varian-Ramos, and M. S. Webster (2009). The relative importance of male tail length and nuptial plumage on social dominance and mate choice in the Red-backed Fairy-wren *Malurus melanocephalus*: Evidence for the multiple receiver hypothesis. *Journal of Avian Biology* 40: 559–568.
- Kisilevsky, B. S., S. M. Hains, C. A. Brown, C. T. Lee, B. Cowperthwaite, S. S. Stutzman, M. L. Swansburga, K. Leec, X. Xied, H. Huangd, H-H. Yed, et al. (2009). Fetal sensitivity to properties of maternal speech and language. *Infant Behavior and Development* 32:59–71.
- Kleindorfer, S., C. Evans, D. Colombelli-Négrel, J. Robertson, M. Griggio, and H. Hoi (2013a). Host response to cuckoo song is predicted by the future risk of brood parasitism. *Frontiers in Zoology* 10:30.
- Kleindorfer, S., C. Evans, M. Mihailova, D. Colombelli-Négrel, H. Hoi, M. Griggio, K. Mahr, and J. Robertson (2013b). When subspecies matter: Resident Superb Fairy-wrens (*Malurus cyaneus*) distinguish the sex and subspecies of intruding birds. *Emu* 113:259–269.
- Kleindorfer, S., H. Hoi, C. Evans, K. Mahr, J. Robertson, M. E. Hauber, and D. Colombelli-Négrel (2014a). The cost of teaching embryos in Superb Fairy-wrens. *Behavioral Ecology* 25:1131–1135.
- Kleindorfer, S., C. Evans, and D. Colombelli-Négrel (2014b). Females that experience threat are better teachers. *Biology Letters* 10:20140046.
- Konishi, M. (1965). The role of auditory feedback in the control of vocalization in the White-crowned Sparrow. *Zeitschrift Fur Tierzucht und Zuchtungsbiologie* 22:770–783.
- Lachlan, R., and S. Nowicki (2012). How reliable is song learning accuracy as a signal of male early condition? *The American Naturalist* 180:751–761.
- Langmore, N. E. (2013). Fairy-wrens as a model system for studying cuckoo–host coevolution. *Emu* 113:302–308.
- Langmore, N. E., A. Cockburn, A. F. Russell, and R. M. Kilner (2009). Flexible cuckoo chick-rejection rules in the Superb Fairy-wren. *Behavioral Ecology* 20:978–984.
- Langmore, N. E., S. Hunt, and R. M. Kilner (2003). Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* 422:157–160.
- Langmore, N. E., G. Maurer, G. J. Adcock, and R. M. Kilner (2008). Socially acquired host-specific mimicry and the evolution of host races in Horsfield's Bronze-cuckoo *Chalcites basalus*. *Evolution* 62:1689–1699.
- Legendre, P., and L. Legendre (1998). *Numerical Ecology*. Elsevier, Amsterdam, The Netherlands.
- Liu, W-C., J. W. Rivers, and D. J. White (2015). Vocal matching and intensity of begging calls are associated with a forebrain song circuit in a generalist brood parasite. *Developmental Neurobiology*. doi:10.1002/dneu.22348.
- Margraf, N., and A. Cockburn (2013). Helping behaviour and parental care in fairy-wrens (*Malurus*). *Emu* 113:294–301.
- Moon, C., H. Lagercrantz, and P. K. Kuhl (2013). Language experienced in utero affects vowel perception after birth: A two-country study. *Acta Paediatrica* 102:156–160.
- Moskát, C., M. Bán, and M. E. Hauber (2014). Naïve hosts of avian brood parasites accept foreign eggs, whereas older hosts fine-tune foreign egg discrimination during laying. *Frontiers in Zoology* 11:45.
- Mulder, R. A., P. O. Dunn, A. Cockburn, K. A. Lazenby-Cohen, and M. J. Howell (1994). Helpers liberate female fairy-wrens from constraints on extra-pair mate choice. *Proceedings of the Royal Society of London, Series B* 255:223–229.
- Nottebohm, F. (1969). The song of the Chingolo, *Zonotrichia capensis*, in Argentina: Description and evaluation of a system of dialects. *The Condor* 71:299–315.
- Nowicki, S., S. Peters, and J. Podos (1998). Song learning, early nutrition and sexual selection in songbirds. *American Zoologist* 38:179–190.
- Nowicki, S., and W. A. Searcy (2014). The evolution of vocal learning. *Current Opinion in Neurobiology* 28:48–53.
- Nowicki, S., W. Searcy, and S. Peters (2002). Brain development, song learning and mate choice in birds: A review and experimental test of the “nutritional stress hypothesis.” *Journal of Comparative Physiology A* 188:1003–1014.
- Oh, K. P., and K. L. Shaw (2013). Multivariate sexual selection in a rapidly evolving speciation phenotype. *Proceedings of the Royal Society of London, Series B* 280:20130482. doi.org/10.1098/rspb.2013.0482
- Payne, R. B. (1982). Ecological consequences of song matching: Breeding success and intraspecific song mimicry in Indigo Buntings. *Ecology* 63:401–411.
- Ranjard, L., M. Anderson, M. Rayner, R. Payne, I. McLean, J. Briskie, H. Ross, D. Brunton, S. Woolley, and M. Hauber (2010). Bioacoustic distances between the begging calls of brood parasites and their host species: A comparison of metrics and techniques. *Behavioral Ecology and Sociobiology* 64:1915–1926.
- Rose, G. J., F. Goller, H. J. Gritton, S. L. Plamondon, A. T. Baugh, and B. G. Cooper (2004). Species-typical songs in White-crowned Sparrows tutored with only phrase pairs. *Nature* 432:753–758.
- Rowley, I., and E. Russell (1997). *Fairy-wrens and Grasswrens (Maluridae)*. Oxford University Press, New York, NY, USA.
- Sharp, S. P., A. McGowan, M. J. Wood, and B. J. Hatchwell (2005). Learned kin recognition cues in a social bird. *Nature* 434: 1127–1130.
- Shizuka, D. (2014). Early song discrimination by nestling sparrows in the wild. *Animal Behaviour* 92:19–24.
- Spencer, K. A., K. L. Buchanan, A. R. Goldsmith, and C. K. Catchpole (2003). Song as an honest signal of developmental stress in the Zebra Finch (*Taeniopygia guttata*). *Hormones and Behavior* 44:132–139.
- Treisman, M. (1978). Bird song dialects, repertoire size, and kin association. *Animal Behaviour* 26:814–817.
- Uy, J. A. C., R. G. Moyle, and C. E. Filardi (2009). Plumage and song differences mediate species recognition between incipient flycatcher species of the Solomon Islands. *Evolution* 63:153–164.
- Varian-Ramos, C. W., J. Karubian, V. Talbott, I. Tapia, and M. S. Webster (2010). Offspring sex ratios reflect lack of repayment

- by auxiliary males in a cooperatively breeding passerine. *Behavioral Ecology and Sociobiology* 64:967–977.
- Webster, M. S., J. Karubian, and H. Schwabl (2010). Dealing with uncertainty: Flexible reproductive strategies by a tropical passerine bird in an unstable environment. *Advances in the Study of Behavior* 42:123–153.
- Webster, M. S., K. A. Tarvin, E. M. Tuttle, and S. Pruett-Jones (2004). Reproductive promiscuity in the Splendid Fairy-wren: Effects of group size and auxiliary reproduction. *Behavioral Ecology* 15:907–915.
- Webster, M. S., C. W. Varian, and J. Karubian (2008). Plumage color and reproduction in the Red-backed Fairy-wren: Why be a dull breeder? *Behavioral Ecology* 19:517–524.
- Woodgate, J. L., M. M. Mariette, A. T. Bennett, S. C. Griffith, and K. L. Buchanan (2012). Male song structure predicts reproductive success in a wild Zebra Finch population. *Animal Behaviour* 83:773–781.