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# Vertical transmission of learned signatures in a wild parrot

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Learned birdsong is a widely used animal model for understanding the acquisition of human speech. Male songbirds often learn songs from adult males during sensitive periods early in life, and sing to attract mates and defend territories. In presumably all of the 350+ parrot species, individuals of both sexes commonly learn vocal signals throughout life to satisfy a wide variety of social functions. Despite intriguing parallels with humans, there have been no experimental studies demonstrating learned vocal production in wild parrots. We studied contact call learning in video-rigged nests of a well-known marked population of green-rumped parrotlets (*Forpus passerinus*) in Venezuela. Both sexes of naive nestlings developed individually unique contact calls in the nest, and we demonstrate experimentally that signature attributes are learned from both primary care-givers. This represents the first experimental evidence for the mechanisms underlying the transmission of a socially acquired trait in a wild parrot population.

**Keywords:** ontogeny; vocal learning; spectrographic cross-correlation and principal coordinates; Psittacidae; Venezuela

## 1. INTRODUCTION

Parrots are celebrated vocal linguists in captivity [1], but how this ability functions in the wild remains unclear [2,3]. All wild parrots studied to date show evidence of signature contact calls that help individuals to distinguish neighbours [4], sexes [5], mates [6,7] and population members [4,8,9]. Playback experiments in several species have shown rapid modification of signature calls during adult vocal interactions [4,10,11], implying that the ability to instantaneously imitate conspecific calls may play a role in fission–fusion negotiations of wild flocks. At the population level, yellow-naped amazons (*Amazona auropalliata*) maintain geographical dialects in contact calls, despite clear evidence for gene flow across dialect boundaries [8,12]. This strongly suggests social learning of population-specific contact calls as individuals migrate from one dialect area to another. It also implies that locally hatched juveniles must have a mechanism for acquiring population-specific contact calls. However, nestling vocal ontogeny has never been studied in wild parrots.

Recent work in captive colonies of spectacled parrotlets (*Forpus conspicillatus*) showed that adults have signature contact calls used in individual recognition [13]. Playback experiments also suggested that vocal signatures are assigned to family members [14]. If true, this would be an intriguing parallel with humans, in which vocal development is often contemporaneous with parents naming infants. However, one alternative that might appear to be vocal labelling would occur if juveniles acquired their own signature calls independently of parents and siblings, and family members later emulated these calls to solicit attention of a focal individual. Another alternative that might also give the appearance of vocal labelling is if parents provide a variety of signature templates to offspring and, as a result, facilitate individual acquisition of a particular signature call, but without directed labelling.

To discriminate between these alternatives in a wild parrot population, we studied contact calls given by adult and experimentally fostered nestling green-rumped parrotlets (*F. passerinus*) in Venezuela. To control for parents mimicking independently derived nestling contact calls, we compared contact calls given by parents early in brood development with the contact calls of nestlings that emerged later in ontogeny. Our results represent the first field data to identify the factors involved in the vertical transmission of a socially acquired trait in free-ranging parrots.

## 2. MATERIAL AND METHODS

### (a) *Nesting and cross-fostering*

The social system of green-rumped parrotlets has been studied since 1988 at Hato Masaguaral (8°31′ N, 67°35′ W), state of Guarico, Venezuela [7,15,16]. The habitat consists of tropical savannah, gallery forest and pastures where parrotlets commonly breed in 106 polyvinyl chloride tubes (1 m length, 0.1 m diameter) lined with hardware cloth. We randomly selected 17 nests of 34 colour-banded adults between June and December in 2007 and 2008. Based on pedigree analysis from 1988 onwards, average relatedness coefficients of all breeding adults studied were 0.000 and 0.003 in 2007 and 2008, respectively ($n = 6692$ individuals) [17]. Twelve nests were selected for cross-fostering; pedigrees were used to assure that reciprocating adults were not closely related. Three of these nests failed before any young fledged and were excluded from analysis. Parrotlets in this

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population have low extra-pair paternity (less than 5%) [18] and we assumed that on average fathers were significantly more genetically related to individuals in their nest than to nestlings at other nests. Donor/recipient nests were on average 304 m from each other and out of earshot (±s.d. = 189 m, range = 166 m), and had similar first egg dates (average difference = 1 day) and clutch sizes (average difference = 1 egg). When clutch sizes differed among donor/recipient nests, we added wax-filled parrotlet egg(s) from other nests to make them equal after the exchange took place. Exchanges took less than 10 min to perform. Eight additional nests served as controls; we similarly removed eggs, but returned them without swapping with eggs at other nests. Laying and hatching dates were estimated from nest checks conducted at 3-day intervals. Eggs and nestlings were marked with non-toxic felt-tip markers. We sexed nestlings by plumage differences, weighed them and measured their wing-chords, and banded them prior to fledging.

### (b) *Audio–video recording*

We made weekly recordings at the nine experimental and eight control nests throughout nestling development. A few days before recordings began, we mounted a video camera (black and white CCD 22 mm, Supercircuits, TX, USA, or a colour DCR-DVD610 camcorder, Sony, Japan) inside the nest cavity. In the same housing, a SM57 directional microphone (Shure, Niles, IL) was mounted and pointed directly at the nest. Parents went about their normal feeding regime within a few hours and there were no cases of abandonment that could be attributed to the AV equipment placed inside nest tubes. Outside the nest, we filmed with a zoom colour 3CCD camcorder (Gl2, Canon, NY, USA) to videotape the parents' arrivals and departures from the nest, and a directional microphone (Sennheiser MKH816, Wedemark, Germany) recorded parents' calls outside the nest. Video streams from both cameras were sent to a video multiplexer (4CQ Everplex, Everfocus, Taipei, Taiwan) and the multiplexed video stream then fed into a Hi8 video camcorder (Sony GVA500). Both microphone feeds were pre-amplified (Mix-Pre, Sound Devices, Reedsburg, WI, USA) and fed into the same Hi8 camcorder using the left and right stereo channels. Standard recording mode was used to record on a Sony HMP HI8 120 or on a Fuji MP HI8 120 cassette tape. Tapes were digitized the same day using an analogue-to-digital converter (ADVC110 Canopus, Grass Valley, Nevada City, CA, USA) and captured on a Macbook laptop computer using FINAL CUT PRO [19], set for 16 bit, 48 kHz audio and 30 frames per second video sampling rates. Audio and video were saved as MOV files. SOUND TRACK PRO [20] was used to identify particular video sequences (while perusing spectrograms) in which a target individual vocalized (as evidenced by bill movements), at which point relevant portions of audio were extracted and archived as WAVE files for spectrographic analysis. The two microphones were more than 5 m apart, so signal arrival times at each microphone were used to determine the source of vocalizations when two individuals vocalized simultaneously, but were different distances from each microphone. To standardize spectrographic quality, we restricted analysis to recordings made with the SM57.

### (c) *Call selection*

Adult calls that we analysed were produced before nestlings began making contact calls, and nestling calls were recorded after their body size reached an asymptote [15]. To control for the likelihood that adults may emulate nestling contact calls, we restricted analysis to calls recorded from adults during the first three weeks of nestling development (mean ± s.d. of age of first hatchling = 13 ± 4.6 day, max. age = 21 day), just prior to the time when nestlings begin to produce contact calls. Contact calls were recorded from nestlings beyond 22 days of age (mean age = 29 ± 2.3 s.d.). A total of 4989 calls were analysed (mean = 175 calls per adult pair ± 75 s.d.; mean = 118 calls per brood ± 63 s.d.; see electronic supplementary material, table S1).

### (d) *Spectrographic analysis*

Similarities between adults and nestlings were quantified with spectrographic cross-correlation and principal coordinates (SPCC–PCO) using a custom program [21,22] in MATLAB [23]. Spectrograms were generated using 514-sample fast Fourier transforms (FFT), a Hann sampling window with 50 per cent overlap, and a broadband de-noising algorithm [22]. Spectrograms were band-pass limited to a 0.75–12.5 kHz frequency range for analysis. Some nestlings in 2007 were studied as breeding adults in 2008, and thus data collected across years were not strictly independent, so we analysed spectrograms for each year separately. We cross-correlated all pair-wise combinations of calls within each year, resulting in two matrices containing 3.0 million and 3.2 million unique cross-correlation values for 2007 and 2008, respectively. For illustrative purposes, we produced spectrograms in SYRINX [24] with a 256 FFT and a Hann sampling window.

### (e) *Statistical analysis*

We used PCO analysis on the correlation matrices to extract a series of orthogonal latent variables of the calls (the PCOs) [21,22]. These latent variables described the major axes of variation and were often correlated with traditional spectrographic measurements (e.g. dominant frequency). However, the PCOs have the added advantage of systematically quantifying similarities in the most important dimensions of variability, and their orthogonal nature satisfies independence assumptions in statistical hypothesis testing. Eigenvalues of the first 10 PCOs explained 87 to 88 per cent of the variation, were all greater than 1 and were entered into the model after a forward, stepwise MANOVA (all $p < 0.001$). We used discriminant canonical analysis [25] to determine the combinations of the most salient PCOs for distinguishing calls among social groups (i.e. adults and either biological offspring or cross-fostered nestlings). This method outputs a similarity score for each call (the canonicals). Mean canonical scores were then calculated for each adult, and mates were compared with least-squares regression, which was also used to compare means of nestlings with randomly selected siblings. Mean canonical scores for each breeding pair of adults were paired with the mean of the group of nestlings that they raised. We used general linear models in SAS [26] to test for an effect of the adults' mean canonical scores on the mean canonical scores of the nestlings they raised. We controlled statistically for whether these comparisons included adults and cross-fostered nestlings or parents and biological offspring by including a covariate interaction term (adult canonical × experiment) in the model. The process was repeated for means of individual adults on means of female nestlings; a female-biased nestling sex ratio (0.8) resulted in too few male nestlings to include in statistical comparisons with individual adults. Statistical significance was accepted at $\alpha = 0.05$.

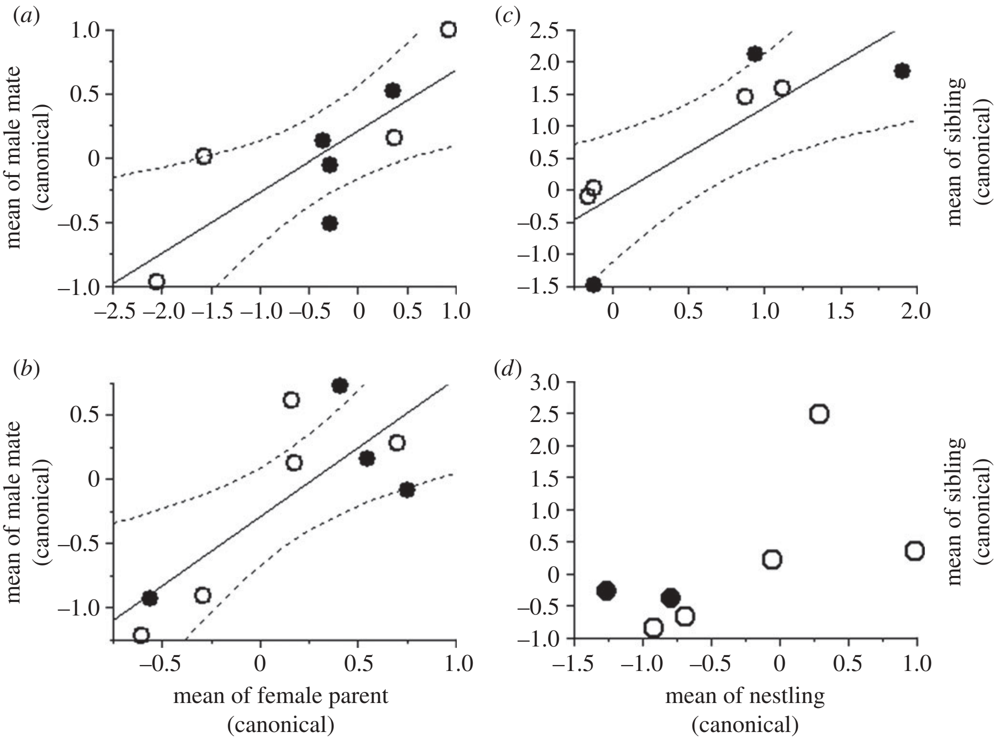

Figure 1. Least-squares regression of contact call similarities within pairs and within sibling groups of green-rumped parrotlet nests. (*a*,*b*) Mean canonical scores of adult males as a function of female mate's canonical scores (*a*) in 2007 and (*b*) in 2008. (*c*,*d*) Mean canonical scores of nestlings as a function of canonical scores of siblings within nests (*c*) in 2007 and (*d*) in 2008. Dotted lines indicate confidence intervals. (*a*) $r^2 = 0.64$, $p < 0.02$; (*b*) $r^2 = 0.62$, $p < 0.01$; (*c*) $r^2 = 0.71$, $p < 0.02$; (*d*) $r^2 = 0.37$, $p < 0.15$.

## 3. RESULTS

Each adult had its own unique contact call that was more similar to its mate than to adults at other nests (figure 1*a*,*b*). Thus, pair members had calls with significantly similar spectral attributes. Nestlings had contact calls that were more similar to their siblings than to nestlings at other nests (figure 1*c*,*d*), but this was significant only in 2007. Thus, although more variable than adults, siblings tended to show convergence in contact call structure. These results justified separately pooling adults and siblings at each nest and comparing group means across nests.

Calls of adults were more similar to the nestlings they raised than to nestlings at other nests, while controlling statistically for cross-fostering (table 1, figure 2*a*,*b*). The interaction of control and cross-fostered groups was weak and non-significant, suggesting that the similarities were not significantly affected by the parents raising cross-fostered nestlings. Adult male calls were more similar to the calls of female nestlings in their nest than to the calls of female nestlings at other nests, but the relationship was only significant in 2007 (table 1, figure 2*c*). Adult female calls were more similar to females in their nest than to female nestlings at other nests, but the relationship was only significant in 2007 (table 1, figure 2*d*). Spectrograms of individuals in cross-fostered and control nests are provided in figure 3.

## 4. DISCUSSION

Our results provide the first experimental evidence for learned vocal production by naive parrots in nature. Nestling contact calls were more similar to the contact calls of their primary care-givers than to adults at other nests, despite half of the nestlings being raised by foster parents. The weak and non-significant interaction of experimental groups (table 1) indicated that the similarities between adults and nestlings were not significantly affected by the adults raising unrelated nestlings. Adult contact calls were recorded before nestlings began to produce their own contact calls, eliminating adult emulation of nestling contact calls as the source of convergence. The combination of results provides strong evidence that the structure of contact calls of both sexes of nestlings is influenced by prior experience with contact-call examples provided by both primary care-givers.

A major distinction between social learning and biological inheritance is the mode of transmission, which in the latter case is vertical [27]. Our study indicates that the structure of parrotlet contact calls is first influenced vertically via social learning. This is facilitated by the nestlings' nutritional dependence on their parents and the vocal exchanges that mediate feeding. However, unlike biological traits, socially acquired traits can also be transmitted horizontally. Our cross-fostering permitted the rearing of nestlings by genetically unrelated adults, but because we transferred entire clutches this method did not alter the genetic relationships within sibling groups. Given the staggered ages of siblings within a brood [15,28], we cannot discount the possibility that calls of older nestlings influenced those of younger siblings independently of adults. To be compatible with our results, however, it must then be the case that at least older nestlings had calls that were directly influenced by those of their primary care-givers, and that similarities between younger siblings and adult calls were due to both direct and indirect effects.

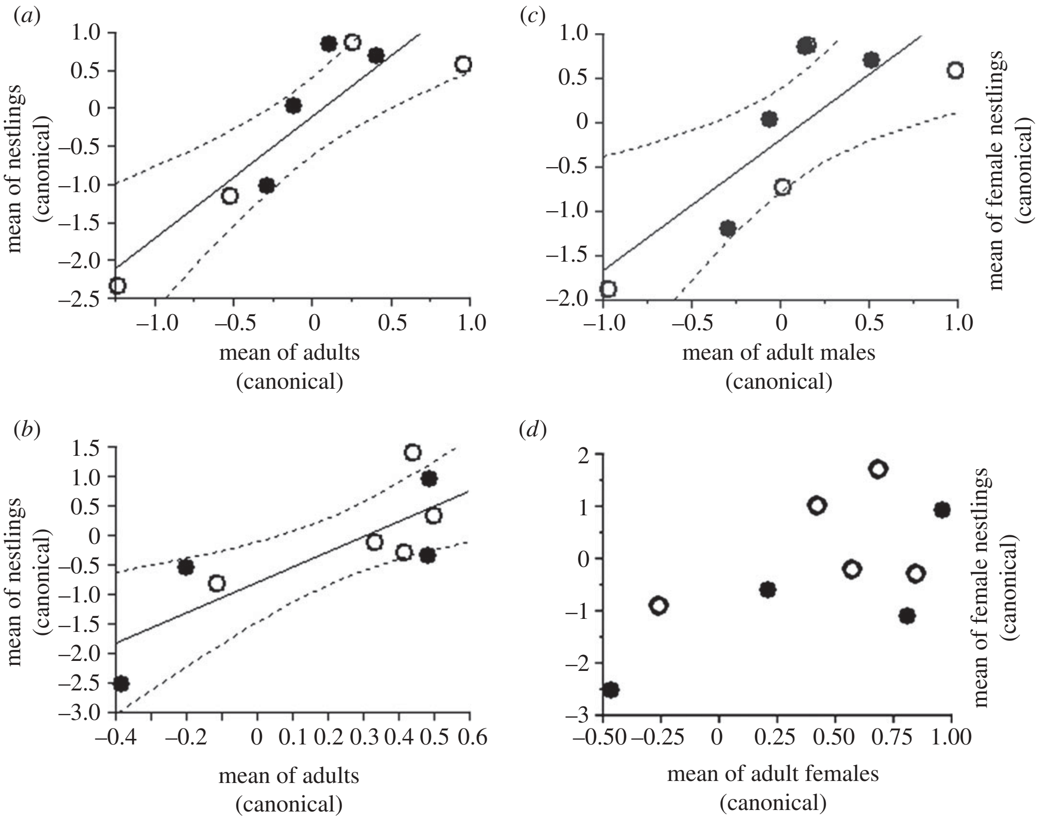

Figure 2. Least-squares regression of contact call similarity for green-rumped parrotlet adults and nestlings. (*a*,*b*) Mean offspring canonical scores within nests as a function of mean canonical scores of adults (*a*) in 2007 and (*b*) in 2008. (*c*) Mean canonical scores of nestling females within nests as function of mean canonical scores of male adults in 2007. (*d*) Mean canonical scores of nestling females within nests as a function of mean canonical scores of adult females in 2008. Dotted lines indicate confidence intervals. Regression coefficients refer to control and experimental nests pooled. (*a*) $r^2 = 0.79$, $p < 0.003$; (*b*) $r^2 = 0.64$, $p < 0.01$; (*c*) $r^2 = 0.65$, $p < 0.02$; (*d*) $r^2 = 0.42$, $p < 0.06$.

Table 1. Results of general linear models using mean canonical discriminant scores of adult contact calls in green-rumped parrotlets (adults) to predict mean canonical scores of nestling contact calls (nestling). The main model is presented first followed by effects of each independent variable; an interaction term (adults × experiment) tested differences between cross-fostered and control groups. Individual adults were regressed against female nestlings (2007: eight nests; 2008: nine nests).

| model (dependent variable) | d.f. | $F$ | $p$ | $r^2$ |
|---|---|---|---|---|
| 2007 | | | | |
| model (nestling) | 2,5 | 10.6 | 0.0159 | 0.81 |
| adults | 1 | 20.6 | 0.0062 | |
| adults × experiment | 1 | 0.6 | 0.4745 | |
| model (female nestling) | 2,4 | 9.47 | 0.0304 | 0.83 |
| adult female | 1 | 18.28 | 0.0129 | |
| adult female × experiment | 1 | 0.67 | 0.4582 | |
| model (female nestling) | 2,5 | 5.71 | 0.0512 | 0.70 |
| adult male | 1 | 10.66 | 0.0223 | |
| adult male × experiment | 1 | 0.75 | 0.4256 | |
| 2008 | | | | |
| model (nestling) | 2,6 | 5.36 | 0.0462 | 0.64 |
| adults | 1 | 10.72 | 0.0177 | |
| adults × experiment | 1 | 0 | 0.9510 | |
| model (female nestling) | 2,6 | 2.51 | 0.1612 | 0.46 |
| adult female | 1 | 4.64 | 0.0746 | |
| adult female × experiment | 1 | 0.38 | 0.5592 | |
| model (female nestling) | 2,6 | 1.52 | 0.2929 | 0.34 |
| adult male | 1 | 2.71 | 0.1510 | |
| adult male × experiment | 1 | 0.33 | 0.5878 | |

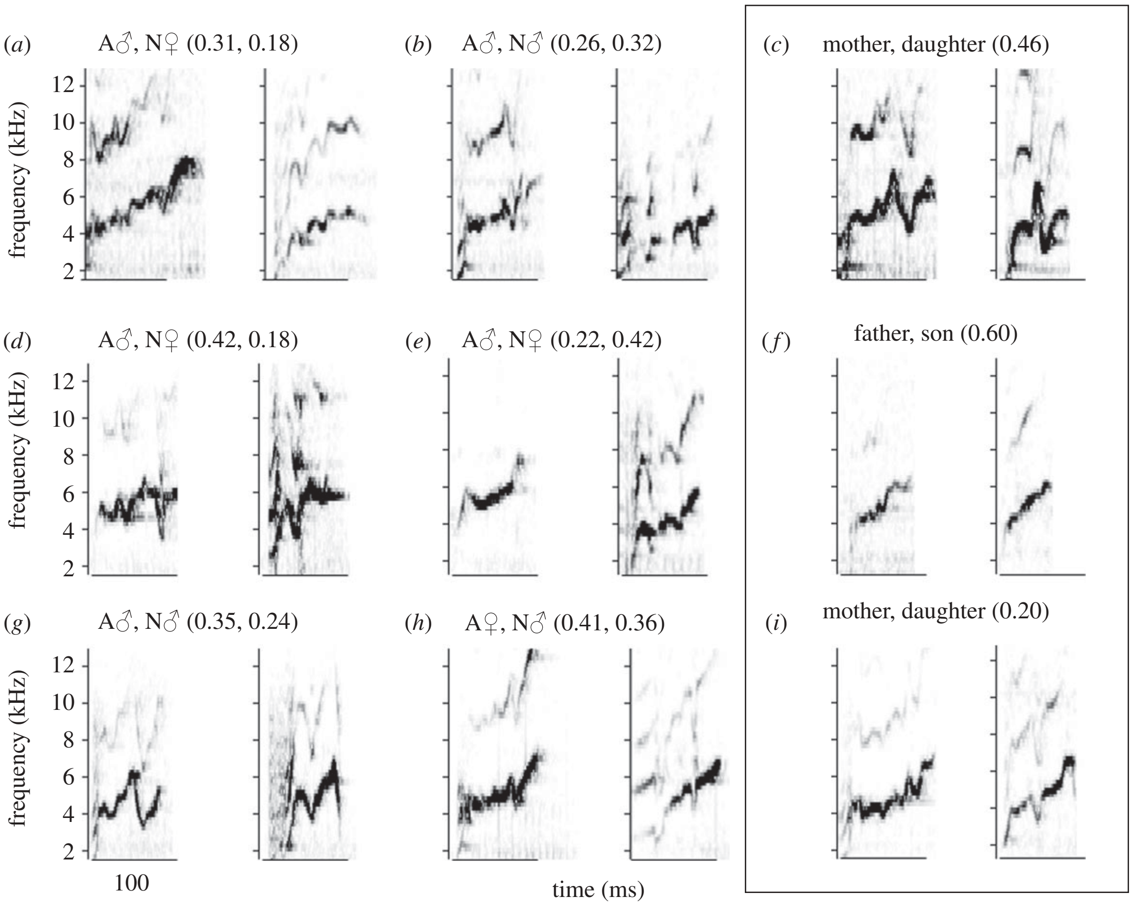

Figure 3. Spectrograms of contact calls from adults and nestlings at 9 nests. In each case the adult's call (A) is paired with the call of the nestling (N) that adult raised from hatching. Adult recordings were taken 1–3 weeks before nestling contact calls were recorded. (*a*,*b*), (*d*,*e*) and (*g*,*h*) each represent pairs of reciprocating cross-fostered nests (e.g. nestling in (*a*) is biological daughter of adult in (*b*)). Cross-correlation coefficients are given parenthetically for each pair of spectrograms, followed by coefficients for parent–offspring comparisons. Examples from control nests are given in (*c*, *f*, *i*). Spectrograms were made with a 256 FFT and a Hann window.

The cognitive processes that underlie avian call learning have received less attention than those associated with song learning [29]. As a result, research on songbirds has often focused on the post-nestling period, when song first emerges. Our results provide one of the clearest examples of learned vocal production in nestlings of wild birds [30,31] and are consistent with results of learning experiments in nestling budgerigars (*Melopsittacus undulatus*) in captivity [32,33]. In the smaller zebra finch (*Taeniopygia guttata*), nestlings fledge weeks earlier than in the two parrots [15,32–34], but all three species show signs of learned vocal production beginning at 3–4 weeks after hatching (this study and [32–36]). This suggests that the time required to establish the neural connections needed for vocal learning is highly conserved [36–38] (see also [39]). Thus, the occurrence of vocal learning during an earlier life-history stage in our study is probably related to the elongated nestling period in parrots [15,38,40,41]. Because different life-history stages are vulnerable to independent sources of selection on learning programmes [42], this may favour parrot nestlings emulating their parents. Whereas the acquisition of song will probably not yield direct benefits before the following breeding season in most nestling songbirds, learning family and individual-level signature calls may be imminently advantageous for nestling parrots because fledging is highly asynchronous, and parents coordinate far-ranging family movements to communal foraging and roosting sites, where unrelated fledglings and predators complicate subsequent parental care.

Extended parental care represents a pivotal point in avian and primate life-history evolution. It allowed for greater brain growth after hatching in parrots [38,41] and greater brain growth post-partum in humans [38,43]. The development of language is often invoked as an explanation for the increase in humans, but how and when language emerges during development is still the subject of debate [43,44]. One developmental milestone is when infants begin to relate adult sound patterns to specific meanings [44,45]. This involves the process of recognizing frequently used sounds in communication channels that somehow engage an infant's attention. Among these sounds, an individual's own name is one of the earliest adult words for which infants show evidence of acoustic pattern recognition [45]. Our study suggests that at least a moderately convergent process may occur in parrots, and that parental provisioning and offspring acquisition of vocal signatures primes juveniles for socialization in a wild parrot population.

Research protocols were approved by the Institutional Animal Care and Use Committee of Cornell University (no. 07-0124) and the Ministerio del Poder Popular para el Ambiente in Venezuela (no. 3437).

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