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Authors

Eggleston, Rory
Viloria, Nurialby
Delgado, Soraya
et al.

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Author for correspondence:

Karl S. Berg

e-mail: karl.berg@utrgv.edu

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Vocal babbling in a wild parrot shows life history and endocrine affinities with human infants

Rory Eggleston¹, Nurialby Vilorio³, Soraya Delgado¹, Astolfo Mata⁴, Hilda Y. Guerrero⁵, Richard J. Kline^{1,2}, Steven R. Beissinger^{6,7} and Karl S. Berg^{1,2}

¹Department of Biology, and ²School of Earth, Environmental, and Marine Sciences, University of Texas Rio Grande Valley, Brownsville, TX, USA

³Departamento de Biología, Universidad de Carabobo, Valencia, Venezuela

⁴Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Caracas, Venezuela

⁵Instituto de Medicina Experimental, Universidad Central de Venezuela, Caracas, Venezuela

⁶Department of Environmental Science, Policy, and Management, and ⁷Museum of Vertebrate Zoology, University of California, Berkeley, CA, USA

KSB, 0000-0002-3648-2991

Prelinguistic babbling is a critical phase in infant language development and is best understood in temperate songbirds where it occurs primarily in males at reproductive maturity and is modulated by sex steroids. Parrots of both sexes are icons of tropical vocal plasticity, but vocal babbling is unreported in this group and whether the endocrine system is involved is unknown. Here we show that vocal babbling is widespread in a wild parrot population in Venezuela, ensues in both sexes during the nestling stage, occurs amidst a captive audience of mixed-aged siblings, and is modulated by corticosteroids. Spectrographic analysis and machine learning found phoneme diversity and combinatorial capacity increased precipitously for the first week, thereafter, crystalizing into a smaller repertoire, consistent with the selective attrition model of language development. Corticosterone-treated nestlings differed from unmanipulated birds and sham controls in several acoustic properties and crystallized a larger repertoire post-treatment. Our findings indicate babbling occurs during an early life-history stage in which corticosteroids help catalyse the transition from a universal learning programme to one finely tuned for the prevailing ecological environment, a potentially convergent scenario in human prelinguistic development.

1. Introduction

Vocal babbling occurs at a critical juncture between a genetically based vocal repertoire and one that depends on the prevailing language environment and is central to our understanding of the origins of human spoken language [1–3]. Songbirds have provided important models of how early neuroendocrine networks prime the brain to coordinate learned, complex vocal communication [4–6]. The developmental stress hypothesis posits that song functions as an honest signal of male quality because chronic stress during early development has deleterious effects on brain structure and learning, thus providing females with a window into developmental histories of potential mates [7–9]. Most evidence comes from bird species in north temperate latitudes where sexual selection and migratory behaviour play important roles in life history, social organization and communication strategies [10,11]. Male and female song learning in tropical birds has received less study but appears to be more common compared to temperate counterparts [12]. Parrots are iconic tropical birds, famous for their vocal imitative abilities in both sexes [13,14]. Despite widespread availability as pets and for laboratory research, a vocal babbling stage in development has gone unnoticed in this group and little is known

about how the endocrine system helps to filter and internalize environmental information in a way that makes vocal plasticity adaptive.

There are good reasons to think parrots might differ from the songbird model of vocal development [13–15]. Although both songbird and parrot nestlings undergo disproportionate amounts of brain growth, songbird brains grow more quickly during the nestling period [16] and undergo a stress hypo-responsive period (SHRP) as a result of inactivation of the hypothalamic-pituitary-adrenal axis (HPA) [17]. SHRP buffers rapidly growing brains from deleterious effects of high corticosteroid levels produced by HPA in response to chronic stress (e.g. starvation and disease) [18]. Since many songbirds are open-cup nesters, SHRP can also help reduce movement and conspicuousness of nestlings to potential predators until fledging or nutritional independence, when HPA again becomes reactive and individuals are equipped to confront challenges on their own [17,19]. By contrast, parrots are obligate cavity nesters with a nestling environment that slows and elongates growth and maturation while shielding nestling activity from visual systems of potential predators, which may favour an absence of SHRP [20]. Obligate cavity-nesting limits breeding opportunities and social organization, and results in female incubation beginning with the first egg [21,22]. Early incubation results in extreme hatching asynchrony and greatly staggered ages of nest-mates [23], leading to competitive asymmetries that may also favour early HPA activation [20,24–26]. Thus, ancestral patterns in cavity versus open-cup breeding alter patterns in endocrine functionality in a way that is appropriate to a given life-history stage.

Male songbirds pass through subsong and plastic stages of song development that are analogous to human infant babbling, with vocal imitation first appearing during the plastic stage [3,27]. Whereas plastic song in songbirds begins at sexual maturation, both sexes of parrots begin imitating contact calls of parents during the nestling period, well before fledging and nutritional independence and months before sexual maturity [28–30]. The parrot nestling period thus encompasses both the sensory (auditory learning) and sensorimotor (auditory and vocal production learning) stages of vocal development. It is a life-history stage that emphasizes survival rather than reproduction and provides a unique opportunity to understand how the developmental stress hypothesis generalizes to vocal learning in non-songbirds.

Here we document vocal babbling and report on results of corticosterone (CORT) supplement experiments on vocal development in a marked population of wild green-rumped parrotlets (*Forpus passerinus*) in Venezuela. From audio-video recordings inside specially designed nest cavities, we show that this plastic stage in vocal development is widespread in both sexes and emerges around the time of first contact call production [28–30] and attainment of adult mass and thermoregulatory ability [31]. Modest, daily CORT supplements were implemented for the first week of babbling to test for the effects of exogenous CORT on babbling. If CORT is deleterious to learning, as in songbirds, then CORT-treated individuals might produce less babbling, have reduced repertoire size or postpone or forego the process entirely. If CORT influences babbling during treatment but not post-treatment, CORT may have activational or motivational effects, whereas differences in post-treatment periods would suggest organizational effects [17,32]. If HPA mediates feedback between the social environment and vocal learning circuits that support

babbling, CORT-treated individuals might babble more or have larger repertoires, while controlling for life history, ontogenetic and treatment and post-treatment factors. We found vocal babbling involves a complex suite of life history, ontogenetic and endocrine factors in both sexes.

2. Material and methods

(a) Study site and population monitoring

All experiments were reviewed and approved by the Institutional Animal Care and Use Committee (AUP-19-18), University of Texas Rio Grande Valley and the Ministerio del Poder Popular para el Ecosocialismo y Aguas in Venezuela (no. 1430). Parrotlets were studied at Hato Masaguaral (8° 34' N, 67° 35' W), a 7000 ha ranch and field research station in the State of Guárico, Venezuela during two breeding seasons (2017, 2018). Habitat consists of tropical savannah, gallery forest and cattle pastures. The population has been studied, banded, and nesting monitored during the breeding season (June–December) since 1988 [33], made possible in part by 106 artificial nest-boxes distributed throughout the ranch. Adults were captured in mistnets and given uniquely coloured leg-band combinations. Nest-boxes were checked for contents every 3 days during the breeding season to determine egg-laying, hatching and fledging dates. Monogamous pairs at each nest were identified by unique colour leg band combinations. Eggs and nestlings were uniquely marked with non-toxic felt-tip markers and given unique colour leg band combinations at 25 days post-hatching (dph). Sex of nestlings was determined by noting discrete differences in plumage sexual dichromatism, which appear at *ca* 15 dph [23].

(b) Audio-video recording

Twelve active nests were selected for audio-video (AV) recording and endocrine manipulations. Brood sizes ranged from 3–8 nestlings. Nest-boxes were rigged with a camcorder (Sony FDR-AX33 or Canon Vixia HFG20) placed above the nest entrance providing a clear view of the contents below. AV recording inside nests began when the female ceased brooding (typically when the oldest nestling was one to two weeks old) and continued daily until the last nestling fledged. Recordings were usually conducted during the morning hours. Recording sessions ranged from 2–4 h. AV was recorded as AVCHD files and saved to SD cards. Recordings were downloaded each day and duplicate copies saved to external hard drives.

(c) Audio-video analysis

Nest recordings were analysed using Adobe AUDITION (v. 11, San Jose, California, USA). Video and audio spectrograms were perused, and audio extracted from bouts of babbling by uniquely marked individuals. Bouts were considered babbling if they consisted of two or more structurally discrete types of vocalization (contact calls, begging, etc.) given in the absence of any obvious behavioural context (i.e. during parental absences) and separated by less than 4 s of silence. Babbling was typically low amplitude in comparison to begging or contact calls given during parental interactions.

(d) Spectrographic analysis

Babbling selections were batch exported from Adobe AUDITION and saved as WAV files with 16-bit resolution and 44.1 kHz sample rate. Spectrograms and waveforms of each element (i.e. syllable) of babbling were measured in RAVEN PRO (v. 1.5, Cornell Laboratory of Ornithology, Ithaca, New York, USA). Audio files were band-pass filtered between 1000 and 15 000 Hz to remove

extraneous sounds and increase signal-to-noise ratio. Only high-quality audio (i.e. where vocalizations were not masked by rain, wind, etc.) of babbling vocalizations was used in spectrographic analysis. Spectrograms were created with a Hann window and 270 Fast Fourier Transform (FFT). Analysis focused on eight spectrographic variables that explained significant individual variation based on previous work [29]: average entropy (hereafter entropy), duration (s), centre frequency (Hz), 5% frequency (Hz, hereafter lower frequency), 95% frequency (Hz, hereafter upper frequency), interquartile range bandwidth (Hz, hereafter bandwidth), average slope of the peak frequency contour (Hz s^{-1} , hereafter FM slope) and number of derivative sign changes in the peak frequency contour (hereafter inflection points).

(e) Corticosterone supplements

One nestling from each of the 12 nests was selected for hormone treatment. CORT-treated individuals were dosed with 25 μl (0.125–0.163 mg ml^{-1}) of CORT-ethanol (ETOH) diluted in peanut oil 2017 (eight broods). In 2018 (four broods) the volume and solvent were changed to a 10 μl (0.4075 mg ml^{-1}) dose of CORT-dimethyl sulfoxide (DMSO) diluted in sesame oil to reduce potential nutritional effects on nestlings. Corticosterone crystals (Selleck Chemicals, 99.43% purity) were fully dissolved in ethanol (Sigma Aldrich, 200 proof) or liquid DMSO (Sigma-Aldrich, $\geq 99.9\%$ purity) by vortexing and heating in a water bath at 65°C. The fully dissolved CORT-ETOH (25 mg ml^{-1}) or CORT-DMSO (90 mg ml^{-1}) solution was then added to peanut oil or sesame oil heated to 65°C and mixed by repeated inverting for final concentrations of 0.125 and 0.163 mg ml^{-1} CORT-peanut oil and 0.4075 mg ml^{-1} CORT-sesame oil. In both years CORT-treated nestlings received oral treatment twice daily between 20 and 26 dph. This dose meant that each nestling in each year received a total daily exposure of approximately 8 μg of CORT per day, during the weeklong treatment period. Previous work indicated this would amount to the equivalent of endogenous CORT produced during two additional parental feedings per day [20]. A control solution was given to sham (hereafter oil) nestlings at the same dosage as that of the experimental nestlings (25 μl oil-ETOH or 10 μl oil-DMSO, twice daily for 7 days). Both CORT-oil mixture and sham treatments were administered by inserting a 25 μl (2017) or 10 μl (2018) Hamilton syringe directly into the orofacial cavity. A control nestling was chosen based on the hatch order of the treatment groups to standardize effects of the hatching sequence. All nestlings were measured daily during treatment.

(f) Statistical analysis

Statistical analysis was conducted in SAS (v. 9.4, SAS Inc., Cary, North Carolina, USA). Centre, lower, and upper frequency, bandwidth, duration and inflection points were \log_{10} transformed to normalize distributions, whereas average slope and entropy did not require transformation. Generalized linear mixed models were used to test for differences in babbling structure based on treatments and a suite of life-history variables. Treatment (CORT, oil or control), treatment period (during treatment 20–26 dph or after treatment 27 dph until fledging, range 29–36 dph), brood size (small = 3–4 nestlings, medium = 5–6 nestlings or large = 7–8 nestlings), hatch order (early, middle, late), sex (female or male) and age (dph) were included as fixed effects. Individual brood (i.e. nest) was included as a random effect to control for repeated measures of nestlings in the same brood. All eight spectrographic measurements were modelled as a Gaussian response distribution linked to an identity function [34]. Models were run for each of the spectrographic variables and each main factor separately (electronic supplementary material, table S1). We initially tested 28 models involving different combinations of explanatory factors and interaction effects. Akaike information criteria (AIC) scores

from each model were used to rank models according to their AIC weights [35] (electronic supplementary material, table S1). For each dependent variable, we report the 99% confidence subset (all models within the model set that contribute to a cumulative AIC weight of 99%). Complete model sets are provided in the electronic supplementary material, table S1. Statistical significance was accepted at $\alpha = 0.05$.

Repertoire size was estimated with *k*-means clustering in JMP (v. 13.0, SAS Inc., Cary, North Carolina, NC). Clustering analysis was based on principal component scores for eight spectrographic measurements to determine discrete call types and objectively quantify repertoire size in each individual and at each stage in development. Cubic clustering criterion (CCC) was used to determine the optimal number of clusters for the entire dataset [36]. This analysis indicated *k* was optimized at 27 clusters (CCC = 4.23, $n = 58\,957$ elements), which was used as a maximal range of *k* to seed each analysis within treatment groups and within treatment periods. CCC was used to optimize *k* in each of the groups and assign clusters to each call. The log total number of elements produced by each individual each day was compared to the log number of clusters (*k*) each day using a quadratic, tri-cubic smoothing function ($\lambda = 0.05$) controlling for treatment groups. Matched pairs were used to determine effects of treatment on the repertoire of each individual before and after treatment, while controlling for repeated measures within nests. The complete dataset of measurements, meta data and associated audio files are provided [37].

3. Results

(a) Babbling in nestling parrotlets

Babbling ensued in parrotlets on average at 21 dph and continued until fledging (29–36 dph). Babbling was low amplitude compared to begging and contact calls, nearly void of bodily movements, and occurred universally in the absence of adult carers, where siblings were the only obvious audience, albeit often asleep (electronic supplementary material, Movies S1,2). In last hatched individuals, babbling occurred without an obvious audience after all siblings had fledged (electronic supplementary material, Movie S3). All nestlings of both sexes babbled extensively (mean female: 1720 \pm s.e.m. 460 elements, $n = 23$ females; male: 1493 \pm s.e.m. 357 elements, $n = 13$ males; $n = 58\,957$ elements, 36 individuals). Bouts had similar durations between sexes (mean females: 5.9 \pm s.e.m. 0.4 s, $n = 1320$ bouts; males: 6.2 \pm s.e.m. 0.6 s, $n = 823$ bouts) and a similar number of elements between sexes (mean females: 30 \pm s.e.m. 2.2 elements per bout, $n = 39\,555$ elements, 1320 bouts; males: 24 \pm s.e.m. 2.0 elements per bout, $n = 19\,402$ elements, 823 bouts). Bouts included a medley reminiscent of nestling begging calls, alarm calls, nestling and adult contact calls, adult warbling, other examples of the adult repertoire and some calls without known functional analogues (figure 1a–f). Calls were usually combined in long strings of elements and devoid of any obvious behavioural context. Bouts of babbling were comprised a repertoire of 27 spectrographically distinct clusters, as identified by *k*-means CCC, which we used as proxies for structurally discrete types of signals used in bouts of babbling (figures 2 and 3).

(b) Effects of corticosterone treatment

Babbling repertoires in the CORT-treated and control groups had similar-sized repertoires during the treatment phase ($k = 24$ –27) (figures 2a–c and 3b), with more ovular clusters (i.e. less definition). During the post-treatment phase all

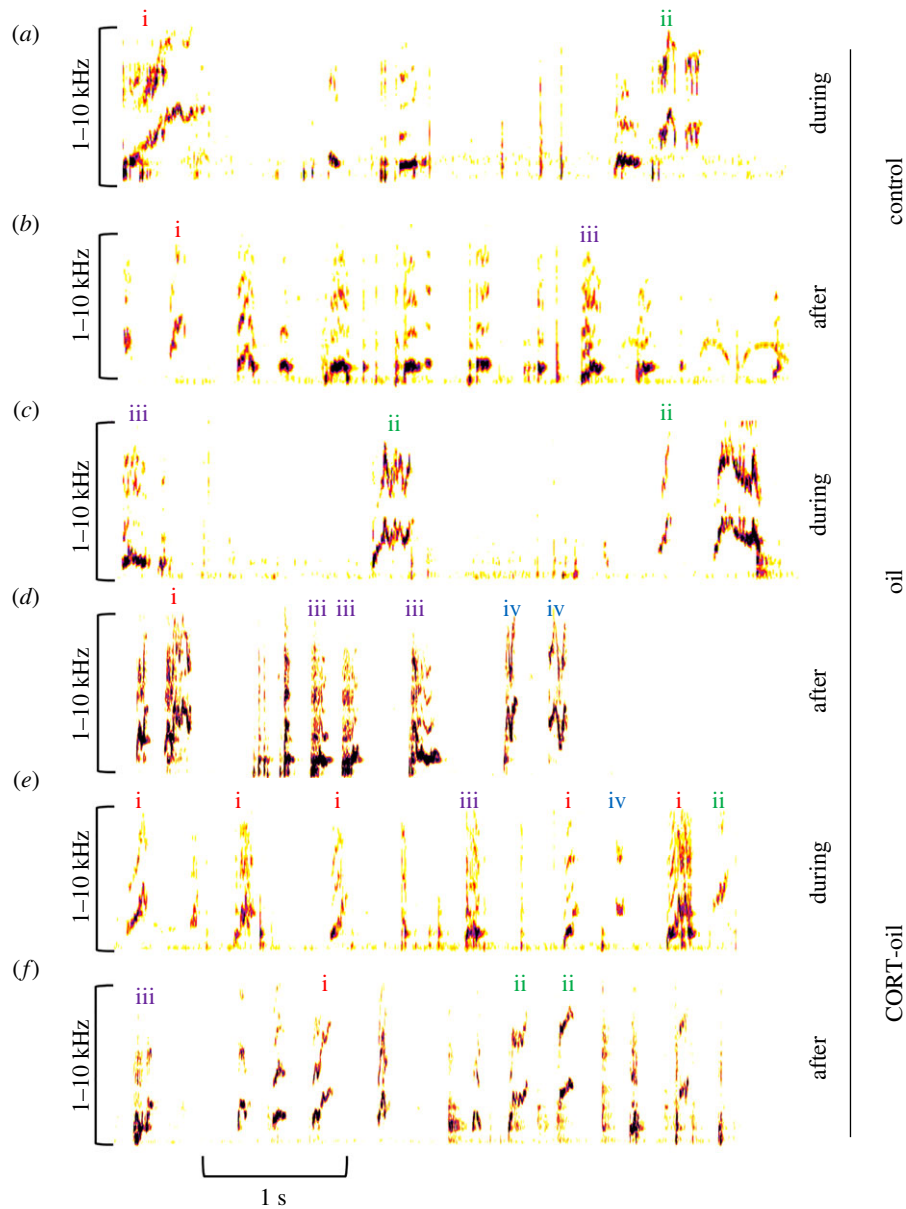


Figure 1. (a–f) Spectrographic examples of portions of bouts of babbling from each treatment group and period. Roman numerals identify analogues of functional call types: i = nestling contact call, ii = adult contact call, iii = adult warble, iv = alarm. (Online version in colour.)

groups had more spherical clusters (i.e. greater definition), but sham control and unmanipulated groups reduced their repertoires (unmanipulated: optimized $k = 17$, $n = 13\,225$; oil: $k = 13$, $n = 18\,812$ elements; figures 2*d,e* and 3*b*), while the CORT-treated group maintained high diversity (optimized $k = 25$, $n = 15\,330$ elements; figures 2*f* and 3). The highest weighted model predicting repertoire size included treatment, treatment period and their interaction (table 1). All individuals in the CORT-treated group increased their repertoire post-treatment (matched pairs, mean difference = 8, $p < 0.001$), while the other groups tended to decrease repertoire size (mean differences unmanipulated = -2, $p < 0.4561$, mean difference sham-control = -9.5, $p < 0.002$; table 1). Thus, controls exhibited an overproduction of signal types during the first week of babbling, followed by crystallization of a smaller set of signal types during the post-treatment period. While CORT-treated birds also exhibited a comparable number of signal types during the first week of babbling, they crystallized a larger repertoire during the post-treatment period.

CORT treatment had a pervasive effect on the acoustic structure of babbling signals. AIC weights indicated that models including CORT treatment were ranked highest for

seven of eight spectrographic variables ($w = 0.82$ – 0.99 ; table 2). Treatment, age, and their interaction were top models in four of the spectrographic variables, while hatching sequence, brood size and sex were also included in some top models (table 2). Thus, a combination of exogenous CORT and life-history factors interacted with different dimensions of acoustic structure and vocal control, suggesting independent sources of selection on babbling repertoires.

4. Discussion

Vocal babbling in parrotlets presents a potentially divergent scenario with subsong and plastic song in closely related songbirds because it occurred in both sexes and during an early life-history stage which emphasizes survival instead of reproduction and one in which HPA plays an important role in growth and maturation [17,38]. Whereas, experimentally induced stress in nestling songbirds often had deleterious effects on learning programmes [8], in parrotlets, CORT supplements resulted in a universal increase in repertoires post-treatment. It suggests CORT produced organizational

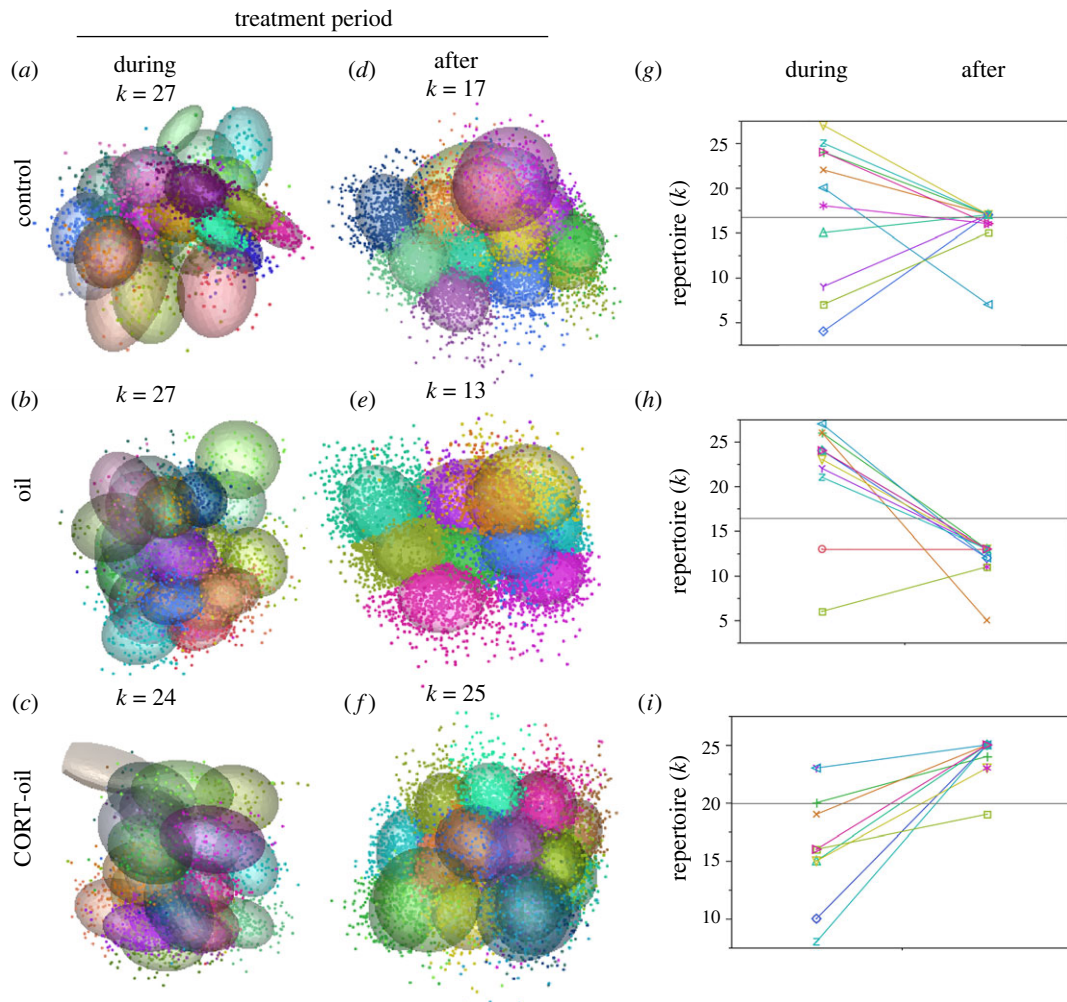


Figure 2. Effects of CORT on babbling and selective attrition. (a–c), k -means clustering of babbling repertoires during CORT treatment based on eight spectrographic measurements. (d–f) During the post-treatment period, untreated (control) and sham control groups (oil) showed a reduced number of clusters (optimized $k = 17, 13$, respectively) (d,e), while the CORT-treated group (f) had high diversity (optimized $k = 25$). Axes are principal components 1 and 2. (g–i) Repertoire sizes of individuals by treatment and treatment period. CORT-treated birds universally increased their repertoire during post-treatment, while controls tended towards decline. Unique symbols and colours differentiate individuals. (Online version in colour.)

effects on learning in both sexes and implicates HPA in the filtering and internalization of auditory information. This differs from the subsong and plastic song stages of male song development, which occur after the nestling period and closer to sexual maturation when seasonal rises in gonadal and non-gonadal sex steroids shape sexual dimorphism in brain and reproductive behaviour [5,6,32]. Organizational effects of brain and behaviour are more likely to occur prior to sexual maturation [32], and our results provide a developmental explanation for why both sexes of parrots are able to use vocal learning in a variety of contexts as adults.

(a) Ecology of parrot babbling

Parrotlet babbling began, on average, at 21 dph the same age at which nestlings produce their first signature contact calls [29,30], which are influenced by contact call templates provided by adult carers [28]. We found nestling and adult-like contact calls were common in babbling repertoires (figure 1), suggesting babbling is probably vulnerable to social influences of adults. However, unlike contact calls that are used to interact with adults [28], babbling was low amplitude, performed in the absence of adults and in the interim period between parental feedings (electronic supplementary material, Movies 1–3). While babbling occurred in lone nestlings, it was observed more frequently when siblings were the only likely audience,

either intended or unintended. Because babbling repertoires included nestling-like contact calls and nestling begging calls (figure 1a–f) and emerged in accordance with the age hierarchy (figure 3) [30], sibling influences on contact calls and babbling repertoires are also possible but will require more research to uncover. Regardless, parrotlet babbling occurred during an earlier life-history stage compared to most songbirds studied to date, was universal in both sexes, did not involve unambiguous vocal exchanges with adults [2,39] and, unlike subsong and plastic song, included a medley of analogues of the nestling and adult functional repertoire. An interesting exception was found in a more basal group of oscine songbirds and one more closely related to the ancestor of the Psittacopasserae, a group that includes parrots and songbirds [40].

(b) Effects of corticosterone manipulations on babbling

Cluster analysis revealed that babbling output and repertoires increased precipitously during their first week and then tended to crystallize (more spherical clusters) on a fewer number of call types (lower optimized k) in the remaining days before fledging (figures 2d,e and 3b). This suggests that our clustering algorithms succeeded in capturing much of the variation in repertoires (figure 3a). Thus, nestlings gradually increased their output and repertoire of call types, followed by a pruning and refining period. This is consistent with the overproduction

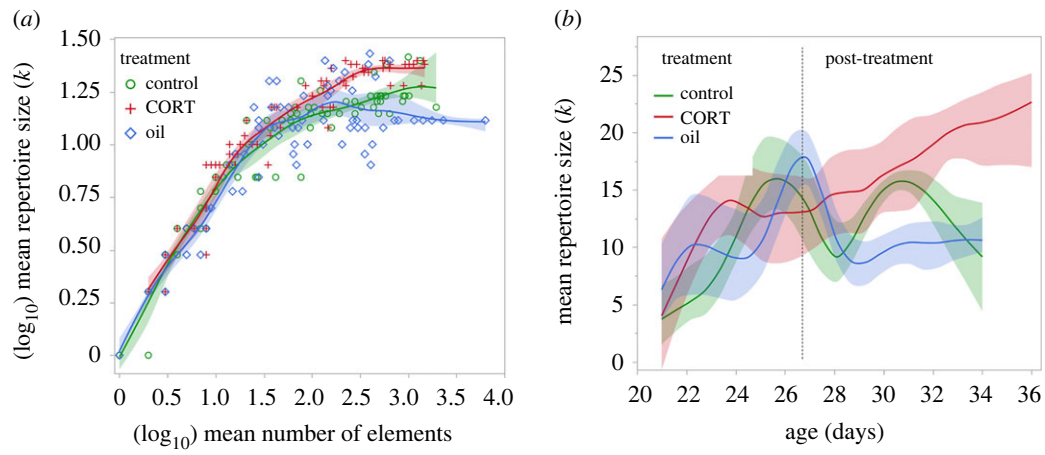


Figure 3. (a) Mean repertoire size per day ($\pm 95\%$ confidence interval (CI)) as function of mean total number of elements of babbling produced each day for each treatment group. (b) Mean repertoire size ($\pm 95\%$ CI) as a function of age and treatment group. All groups increased repertoires during the treatment period. During the post-treatment period, controls and unmanipulated individuals' repertoires declined, while CORT-treated individuals increased repertoires. k is the number of clusters from k -means cluster analysis. (Online version in colour.)

Table 1. Effects of CORT treatment on vocal babbling repertoire size. (Treatment refers to CORT-treated, sham control and unmanipulated groups; period refers to period during CORT-treatment versus post-treatment; random refers to an intercept only model.)

model	d.f.	F	$p <$	k	AICc	Δ AIC	w
I				12	390.4	0	1.00
treatment	2,51	3.61	0.034				
period	1,51	0.96	0.333				
treatment * period	2,51	20.2	0.001				
II				7	426.8	36.39	0.00
treatment	2,53	2.26	0.114				
period	1,53	0.74	0.392				
III				5	430.1	39.75	0.00
treatment	2,54	2.31	0.109				
IV				4	437	46.62	0.00
period	1,55	0.79	0.378				
V					440.4	50.06	0.00
random							

Table 2. Model selection using Akaike information criteria (AIC) for models predicting individual spectrographic attributes. (For each dependent variable, factors and AIC weights (w) are provided for the 99% confidence set. Entire model sets for each analysis appear in the electronic supplementary material, table S1. Hatch and brood refer to sequence and size respectively.)

dependent	rank	model	w
avg slope	1	treatment + hatch + treatment \times hatch	0.99
duration	1	treatment + hatch + sex	0.82
	2	treatment + brood size + treatment \times brood	0.18
centre Hz	1	treatment + age + treatment \times age	0.99
bandwidth	1	treatment + age + treatment \times age	0.99
avg entropy	1	treatment + brood size + treatment \times brood	0.99
inflections	1	treatment + sex + treatment \times sex	0.99
low Hz	1	treatment + age + treatment \times age	0.99
high Hz	1	age	0.82
	2	treatment + age	0.18

and selective attrition model of songbird and mammalian vocal development [1,2,27,41–43]. However, CORT-treated birds tended to skip the pruning (higher k), but not the refining period (more spherical clusters, figure 2f) during the post-treatment period. This result is corroborated by the universal increase in repertoires in the CORT-treated individuals post-treatment, providing strong evidence that CORT altered the pruning and crystallization process. In mammals and birds, juvenile play-like behaviours and the HPA axis are implicated in a neural pruning process in hierarchically organized brain regions that prime social-motivational circuits for the prevailing social environment [44,45]. Play-induced pruning of the repertoire may also be involved in late-developing brain regions that control babbling because babbling is often referred to as vocal play [46] and vocal learning engages social-motivational circuits [4,47,48].

Our supplements involved modest exposure to CORT yet had important effects on parrotlet babbling. This suggests that vocal-production learning processes in both sexes of nestlings are vulnerable to subtle differences in environmental challenges during a life-history stage when siblings are an important aspect of the social and auditory environment [30]. Our findings differed strongly from babbling in most songbirds, which occurs when individuals have dispersed and reached sexual maturation and is shaped by gonadal steroids and interactions with unrelated adults [5,6,32]. It remains to be seen if gonadal steroids also influence vocal babbling in nestling parrotlets, which show sexual dichromatism in plumage at 15 dph [21]. Nevertheless, in this study parrotlets babbled months prior to sexual maturation; probably before the hypothalamic-pituitary-gonadal axis was fully functional and showed a remarkable absence of aggression between siblings, given the extreme age hierarchy [30]. We found some evidence of sex differences in how CORT affected acoustic structure (table 2), which might be caused by gonadal or non-gonadal sex steroids [11,32]. However, it might also be explained by sex differences in glucocorticoid receptor distributions rather than effects of gonadal-steroidal activity [49]. By contrast, nestling parrotlets showed adult-like adrenocortical functionality as early as 13 dph, which is one week before the onset to babbling [20] (this study), and restraint stress responsiveness increased in larger broods [20] that have more complex social environments and greater contact call diversity [30]. Thus, a lack of SHRP in parrotlets may be adaptive if HPA helps tailor the learning and pruning process to levels of complexity in the prevailing social environment. While different from the songbird model, these results do not undermine the developmental stress hypothesis—to the contrary, parrotlet nestlings may be more vulnerable to chronic stress owing to an absence of SHRP. However, it does suggest that benefits of HPA reactivity must be important enough to outweigh the potential costs of increases in allostatic load.

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5. Conclusion

Our understanding of vocal babbling has been primarily derived from studies in captivity (songbirds) or in laboratory (human infants) settings, which often negates following subtle but constant changes in natural song and language development, respectively, that may be influenced by the neuroendocrine feedback with prevailing socioecological environments. Our study of free-ranging parrots indicated that babbling: (i) naturally occurs early in development in both sexes; (ii) is performed with or without an audience, suggesting an internalized role in cognitive development; (iii) is composed of a diverse medley of the adult and nestling repertoire, but not yet integrated into respective functional contexts; (iv) is modulated by corticosteroids; and (v) regularly occurs in the presence of siblings of markedly different age, size and experience levels. Sibling influences on the plastic stage in vocal development have received less attention in songbirds [50], where sibling age hierarchies if they exist, range from a few hours to a few days. Conversely, parrotlet sibling age hierarchies range up to 17 days [23], creating an early social environment characterized by a spectrum of competitive and socio-positive asymmetries that prime the endocrine system for the prevailing learning environment [20,30] (this study), a potentially convergent scenario with the sibling hierarchies' role in human infant language development [51].

Ethics. All experiments were reviewed and approved by the Institutional Animal Care and Use Committee (AUP-19-18), University of Texas Rio Grande Valley and the Ministerio del Poder Popular para el Ecosocialismo y Aguas in Venezuela (no. 1430).

Data accessibility. Data has been made available as electronic supplementary material [52], in tables S1 and S2; and audio files are available at Dryad <https://doi.org/10.5061/dryad.k0p2ngfb3> [37].

Authors' contributions. R.E.: conceptualization, formal analysis, investigation, writing—original draft; N.V.: investigation, project administration, supervision; S.D.: conceptualization, formal analysis, investigation, methodology, project administration, supervision; A.M.: conceptualization, formal analysis, funding acquisition, investigation, methodology, supervision; H.Y.G.: conceptualization, formal analysis, investigation, methodology; R.J.K.: funding acquisition, methodology; S.R.B.: conceptualization, data curation, funding acquisition, investigation, methodology, project administration, resources, writing—review and editing; K.S.B.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, supervision, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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