



## Original Article

# Allo-preening is linked to vocal signature development in a wild parrot

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Allo-grooming networks in primate social groups are thought to have favored the evolution of vocal recognition systems, including vocal imitation in humans, as a more effective means of maintaining social bonds in large groups. Select avian taxa converged on vocal learning, but it is not clear what role analogues of allo-grooming might have played. Unlike allo-grooming in most primates, allo-preening in birds is usually limited to pair-bonds. One exception to this is during nestling development when siblings preen each other, but it is unknown how allo-preening influences vocal learning. We addressed this question in wild Green-rumped Parrotlets (*Forpus passerinus*) in Venezuela. Nestlings learn signature contact calls from adult templates. Large broods, age hierarchies and protracted development in this species create the potential for complex allo-preening networks and a unique opportunity to test how early sociality makes the development of vocal learning labile. From audio-video recordings inside nest cavities and a balanced design of different brood sizes, we quantified allo-preening interactions between marked nestlings, to compare to signature contact calls. Controlling for brood size and age hierarchy, the propensity to preen a larger number of individuals (i.e., out-strength) correlated positively with the age at first contact call. Allo-preening and acoustic similarity matrices did not reveal clear correlations within broods, instead larger broods produced greater contact call diversity. Results indicate that allo-preening elongates the period during which contact calls develop, which might allow individuals time to form a unique signature under the computationally challenging social conditions inherent to large groups.

**Key words:** allopreening, social network analysis, social play, vocal signature, vocal production learning, Venezuela.

Allo-grooming and allo-preening are widespread in mammals and birds respectively and can serve important hygienic (e.g., ectoparasite removal); stress alleviation (e.g., deescalate conflicts, lower glucocorticoid levels); and social signaling functions (e.g., formation and maintenance of social bonds and social hierarchies) (Bradbury and Vehrencamp 2011). Allo-grooming is especially important in maintaining social hierarchies in primates but is less effective in cases where groups are large and more dispersed and is thought to have favored the use of vocal recognition cues (McComb and Semple 2005; Arlet et al. 2015; Kulahci et al. 2015; Dunbar 2017). Vocal signatures are more efficient at monitoring social interactions in larger groups and can be heard over long distances, through dense vegetation and in complete darkness. Vocal imitation in humans had the added benefit of allowing individuals to imitate the vocal signatures of a large number of social companions. Such personalized communication channels likely enable other types of social interactions (foraging, roosting, copulating, etc.), resulting in higher levels of differentiated social

relationships and opportunities for eavesdropping. While evidence is accumulating for the importance of vocal production learning in non-human primates (Lameira 2017; Ghazanfar et al. 2019; Fischer and Hammerschmidt 2020), vocal signature learning is better known among mammals in oceanic dolphins (Nousek et al. 2006; King and Janik 2013), where the need for grooming is attenuated. Vocal signature learning also occurs in select groups of birds (Mundinger 1970; Sharp et al. 2005; Bradbury and Balsby 2016), where preening is an important analogue. However, the linkages between primate grooming and vocal production learning have been difficult to reconcile with the origins of vocal learning in birds because allo-preening, while important, occurs mainly at the pair-bond and not group level—social groups of birds rarely exhibit the number of intense social bonds that characterize many primate societies (Dunbar and Shultz 2007). One exception to this is during early development, but little is known about nestling allo-preening's influences on vocal signature development.

We addressed the question of how sibling allo-preening behavior might relate to vocal signature acquisition in a marked population of Green-rumped Parrotlets in Venezuela. Adult parrotlets use contact calls to navigate complex social groups, including

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reproductive activities between monogamous pairs (Berg et al. 2011); coordination of parent-offspring interactions (Berg et al. 2012); and movements of far-ranging social foraging and roosting congregations (K.S.B., unpublished data). Spectrographic analysis of individuals' contact calls and playback experiments show that adults have individually unique contact calls that can be used to recognize mates (Berg et al. 2011). Nestlings acquire contact calls at on average 3 weeks post-hatching, 1 week prior to fledging (Berg et al. 2013), though there is considerable variation. Cross-fostering experiments showed that nestlings model their contact calls based on a diversity of templates provided by adult caregivers (Berg et al. 2012). It is as of yet unclear the significance of adult contact call repertoires, however, in the closely related Spectacled Parrotlet (*F. conspicillatus*), vocal labeling of social companions has been suggested from laboratory studies (Wanker et al. 2005), in which case contact call repertoires in wild green-rumped parrotlets might include their own vocal signature as well as signatures of related and unrelated individuals with whom they interact on a regular basis. Regardless, it is unclear how each nestling obtains unique signature attributes, given that one monogamous pair of adults care for each brood.

There are several ways that early sociality might foster vocal signature learning in parrotlets. One possibility is that adult caregivers expose the brood to a variety of templates and each nestling chooses one. A nonmutually exclusive explanation is that extreme hatching asynchrony in this species, which can range between 8–24 days (Beissinger and Waltman 1991), confers unique aural experiences on each individual. Both explanations are alone problematic in that they suggest a passive role for nestling learning. Social learning often involves direct social interactions, feedback and motivation, and is often under strong influence by the number of early social bonds (Falk 2009; Hrdy 2009; Konner 2010). While social bonds with parents may suffice, the potential for allo-parenting by older siblings increases significantly in larger broods, which have more exaggerated age hierarchies (Ducouret et al. 2020). We thus focused on allo-preening between nestlings. Adult allo-preening is common during courtship and social bonding (Waltman and Beissinger 1992), within adult male-male pairs (Beissinger 2008) and when adults preen nestlings. Allo-preening involves voluntary use of bill and tongue movements, structures and processes involved in vocal tract movements during parrot vocal production (Dubbeldam 1999; Beckers et al. 2004; Brauth et al. 2006).

We quantified allo-preening, morphological and life history attributes in individuals from different brood sizes to compare to the age at first contact call and the acoustic structure of individuals' contact calls. Given that brood size puts an absolute limit on the number of social companions (i.e., closed networks); siblings' proximity to each other; the underdeveloped nature of extremely altricial nestlings; and the opportunity for random interactions, allo-preening might be un-related to the number of siblings or contact call emergence. Given the age hierarchy, younger siblings might converge on signature attributes at the brood level (Sharp et al. 2005), in which case favored preening partners might have more similar calls. On the other hand, if vocal production learning involves cross-talk between developing auditory-guided vocal control circuits and social-motivational circuits in the forebrain (Nottetbohm and Liu 2010; Syal and Finlay 2011), allo-preening may be more directly related to signature call formation.

## METHODS

### Study site

We studied a wild population of Green-rumped Parrotlets in a seasonally flooded tropical savanna at Hato Masaguaral, State of Gaurico, Venezuela ( $8^{\circ}34'N$ ,  $67^{\circ}35'W$ ). The population has been color-banded and breeding ecology monitored since 1988, facilitated by 120 artificial nest tubes ( $1 \times 0.04$  m, Poly-Vinyl Chloride) distributed throughout the 7000 ha ranch (Beissinger 2008). Breeding attempts occur from June through December coinciding with the wet season. Brood size ranges from 4 to 12 individuals, creating pronounced age hierarchies (Waltman and Beissinger 1992).

### Nest monitoring

Nest cavities were checked at 3-day intervals between 1 June and 30 November in each year to determine laying and hatching dates. Un-banded adults were captured in mistnets and given unique aluminum color leg-band combinations, which were used to identify monogamous pairs at each nest. Nestlings were marked with non-toxic, felt-tipped markers beginning at hatching and measured, weighed and fitted with unique color leg-band combinations at 25 days post-hatching (dph). Sex was determined by noting discrete differences in plumage coloration, apparent by ca. 15 dph (Waltman and Beissinger 1992).

### Audio-video recordings and sibling social interactions

Between 2011 and 2018, multiple breeding attempts were filmed by rigging High Definition (HD) camcorders (HDR CX160, PJ650, Sony Corp., Tokyo, Japan) inside cavities with a clear view of the nest contents below. Audio-Video (AV) was recorded as AVCHD files saved to SD cards. Recordings began daily after adult females ceased brooding (7–15 days after the first nestling hatches) (Waltman and Beissinger 1992), to lessen the likelihood of clutch abandonment, and ended when the last nestling fledged. Recordings began between 0700 and 1000 h and continued for 1–3 h. Recordings were downloaded each day and multiple copies saved to external hard drives.

We quantified sibling social interactions and contact call development in nine nests, selected to provide a balanced design of different brood sizes. Focal broods contained a total of 55 nestlings and were equally distributed among three different brood size categories: three small broods (4 nestlings), three medium-sized broods (6 nestlings), and three large broods (8–9 nestlings). Within-brood ages of nestlings ranged between 1 and 14 dph. Two nestlings died from unknown causes at 5 and 24 dph, respectively. All other nestlings successfully fledged. Two additional broods of two nestlings each were analyzed for contact calls to provide information on unusually small broods but were excluded from social network analysis given the small number of interactants. Adobe Audition (v. 2018, Adobe Inc., San Jose, CA, USA) was used to review video frame-by-frame and quantify social behaviors, while visually perusing audio spectrograms. Because recordings varied in length, data collection was restricted to the first 1.5 h of each video session.

### Allo-preening analysis

Allo-preening was defined as an asymmetrical behavior where one individual (actor) clasps a feather of a nest mate (receiver) in its bill, moving its bill along the longitudinal axis of the feather. Simultaneous, reciprocal allo-preening was rare and treated as two

events with overlapping time signatures. In most cases, recipients (receivers) were tolerant and did not shift position or attempt to elude the actor's advances, suggestive of a socio-positive behavior (*Supplementary Movie 1*). At each behavioral interaction we identified actor, receiver, (i.e., directionality) and duration ( $\pm 0.01$  s) for all dyadic allo-preening events. Data collection on social interactions ended once focal nestlings produced their first contact calls, because our objective was to examine influences of preening on contact call production. We excluded interactions involving an actor younger than 10 dph, because nestling parrotlets lacked feathers prior to this stage (Waltman and Beissinger 1992), as well as events lasting less than 1 second, to exclude incidental interactions.

### Social network analysis

Nestling interactions in the nine broods were analyzed using the iGraph package in R (v3.4.2) to generate metrics of social network structure within each brood. In-degree was calculated by summing the number of sibling dyads where the focal nestling was the receiver and out-degree as the sum of the number of dyads where the focal nestling was the actor (Whitehead 2008). We also calculated the difference in in- and out-degree. Out-strength, a weighted measure of the number of siblings that a focal nestling directly preens (Whitehead 2008), was calculated using the duration of all events in each dyad. In-strength was similarly the weighted number of dyads in which a focal individual was the receiver. Edge Density, a measure of the proportion of how many siblings interacted with one another, out of the maximum number of potential dyads (Wey et al. 2008), was calculated for each brood.

### Age at first contact call

Adobe Audition was used to visualize spectrograms and extract audio examples of contact calls made by individually identified nestlings in the nine broods, as well as the two-nestling broods. The minimum age at which each nestling produced contact calls was used as an estimate of the age at first contact call production, while acknowledging that nestlings could have produced contact calls outside of our recording sessions. However, the likelihood of this is countered by the strong tendency for nestlings to use contact calls, once they begin to produce them, upon arrival of adult caregivers (Berg et al. 2013) (*Supplementary Movie 2*) and our sampling captured several parental visits per day. We also calculated the age at first contact call as proportion of the age at fledging for each individual, to standardize developmental stages. However, because results did not differ and age is relevant to auditory learning periods, we report results based on the absolute age in dph.

### Spectrographic analysis of contact calls

Only high-quality recordings of contact calls (e.g., no overlapping signals from other individuals or extraneous noises) were used in spectrographic analysis. Calls were batch-extracted and saved as Waveform Audio (WAVE) files with a 16-bit depth, 44.1 kHz sample rate and imported into Raven (V. 1.4, Cornell Lab of Ornithology, Ithaca, NY) for spectrographic analysis. Fast Fourier Transform (FFT) was used to select spectrogram parameters that provided an optimal tradeoff between temporal and frequency resolution (FFT = 256). To standardize any developmental differences, only contact calls produced by nestlings over 25 dph were included in spectrographic analysis. We extracted on average of 48 calls per individual ( $\pm 20$  SD,  $N = 55$  individuals) and an average of 290 calls for each of the nine broods where preening was quantified ( $\pm 141$  SD,  $N = 2606$  calls). Calls were band-pass filtered between

500 and 12,500 Hz to remove extraneous sounds. Spectrographic Cross-Correlation (SPCC) was used to quantify similarity in acoustic structure of all pairwise comparisons of calls within broods. Raven outputs a similarity matrix of cross-correlation coefficients (0.00–1.00), which was then used to calculate average correlation coefficients between all sibling dyads within a brood. This similarity matrix was used to compare to social network matrices based on total duration of preening events and the frequency of events. In a separate analysis, we selected 10 calls from each individual and conducted cross-correlation (586 calls) to allow for comparisons of acoustic structure across different brood sizes (171,112 pair-wise comparisons; see details below). This included the 55 individuals referenced above, in addition to four nestlings, two from each of two broods ( $N = 59$  nestlings).

### Statistical analysis

Statistical analyses were conducted in SAS (v9.4, SAS Institute Inc., Cary, NC). Generalized Linear Mixed Models (GLMMs) were used to test relationships between age at first contact call production (dependent variable) and a suite of life history, behavioral and morphological variables as fixed factors. Individual brood of nestlings was included as a random effect in each model to control for repeated measures of group identity. Absolute measures of preening and out- and in-strength were normalized by dividing by the maximum metrics in each brood. A correlation matrix indicated that frequency and duration of preening by actors were highly correlated with each other and with out-strength (all  $> R = 0.92$ ,  $P < 0.001$ ). Tolerance values (0.0007–0.15) and Variation Inflation Factors (VIF) (all  $> 6.5$ ) also indicated strong multicollinearity. As such, strength and absolute measures were not combined in the same models. Similarly, in-strength was highly correlated with the frequency and duration of preening received (all  $R > 0.91$ ,  $P < 0.001$ ; Tolerance: 0.01–0.17; VIF: all  $> 6$ ) and not combined in the same model. Because brood size was strongly correlated with in-degree and out-degree (all  $R > 0.97$ ), degree measures were excluded from further analysis. The remaining factors were not strongly correlated (all  $R < 0.70$ ) and included 6 preening variables and 8 life history or morphological variables that might plausibly relate to development in general or that exclusions of which would violate independence assumptions (i.e., brood size). We included a random effect, intercept only model (i.e., null model) for comparison. We initially used each factor in separate models and conducted Akaike Information Criteria (corrected for small sample sizes, AICc) to rank models according to AICc weights. This analysis indicated four factors were important in explaining variation in age of first contact call (top 95% of weights): out-strength, out-preen frequency and duration, and brood size. Based on this initial analysis we built 31 models using factors, combined with brood size, hatch order and their interaction, as well as simpler models. From this analysis, we report results of AIC analysis and Evidence Ratios (Garamszegi et al. 2009; Burnham et al. 2011) for each model and effect sizes and confidence intervals for each factor in the top five models representing a 95% confidence subset (Burnham and Anderson 2004). A version of Cohen's  $f^2$  was used to estimate effect size of continuous regressors on the dependent continuous variable age of first contact call ( $f^2 = R^2_{AB} - R^2_A / 1 - R^2_{AB}$ ), where  $B$  is the continuous regressor (e.g., out-strength) and  $A$  is the portion of the model including categorical variables (e.g., brood size, hatch sequence and interaction);  $R^2_{AB}$  is the portion of the variance accounted for by the full model and  $R^2_A$  is the portion of the variance accounted for by the categorical variables (Selya et al. 2012).  $R^2$  was calculated

using the residual variance of the full model ( $V_{\text{full}}$ ) and the residual variance of the model without the regressor ( $V_{\text{null}}$ ):  $R^2 = V_{\text{null}} - V_{\text{full}} / V_{\text{full}}$ . Full and null models were run while holding constant the random effects of brood identity. Confidence Intervals for  $\beta$  were calculated as  $\beta / (1 \pm \beta)$  (Sokal and Rohlf 2012). For categorical variables and interaction terms, we calculated the difference between each parameter and the overall mean ( $\text{Diff} = \mu_i - \mu$ ) from model least square means and then pooled the differences for each factor ( $\text{Diff}_p = (\text{Diff}_{\text{max}} - \text{Diff}_{\text{min}}) / 2$ ). The pooled SD for each factor was calculated as  $\text{sqrt}((\sum_k^i (ni - 1) * (\text{SD}_p^2)) / (n - k))$ , where  $k$  is the number of levels in each group. We used a version of Cohen's effect size  $f_c$  for a multi-level, multifactor model with means evenly distributed between two extremes, as  $\text{sqrt}(k + 1 / k + 2) * v_{\text{min}} / 2$ , where  $v_{\text{min}}$  is the ratio of the pooled differences to pooled SDs ( $\text{Diff}_p / \text{SD}_p$ ) (Sokal and Rohlf 2012). SE<sub>es</sub> for each effect size were calculated as  $s_qr_t((\sum_k^i (ni + nj..k)) / (ni * nj..k)) + f_c^2 / 2 * (\sum_k^i (ni - k))$ . Lower and upper 95% Confidence Intervals were calculated as  $f_c \pm 1.96 * \text{SE}_{\text{es}}$  (Nakagawa and Cuthill 2007). This analysis thus allowed us to assess each model's weighted AIC score and Evidence Ratios;  $P$ -values for likelihood of estimates within each model; standardized effect sizes for each factor therein and the precision of these estimates based on whether confidence intervals did not include zero at  $\alpha = 0.05$ . A similar analysis was used to determine predictors of in-strength. Statistical significance was determined at  $\alpha = 0.05$ .

A Quadratic Assignment Procedure (QAP) correlation test was used in UCINET (v6) (Borgatti et al. 2002) to test for sibling social influences on contact call structure by comparing matrices based on duration of allo-preening to similarity matrices of contact call structure from SPCC (10,000 permutations). Summing events involving naive receivers that had not yet produced contact calls generated allo-preening matrices. Allo-preening matrices were weighted by total duration and frequency of interactions per dyad for each brood. Given that comparisons of multiple broods could increase the likelihood of false positives, we calculated False Discovery Rates (FDR) (Benjamini and Hochberg 1995) to adjust statistical significance thresholds. This analysis indicated an FDR  $\alpha = 0.0026$ , which was used to determine statistical significance.

Because SPCC matrices within broods are not comparable across broods, we also cross-correlated 586 calls, 10 from each of 59 individuals, to test how vocal diversity changes across brood sizes. We used Multi-Dimensional Scaling in JMP Pro (v.2013 SAS) to analyze the SPCC matrix, which produced new latent variables (dimensions). The first two dimensions were used in a  $k$ -means cluster analysis to identify independent clusters as proxies for different signal classes. The number of cluster seeds that provided nonoverlapping confidence circles were assigned to each call. Cluster assignments were then used to calculate Shannon-Wiener Diversity ( $-\Sigma = p_i \ln p_i$ ) to estimate how evenly each brood's repertoire was distributed across clusters and to compare to brood size.

## RESULTS

### Allo-preening

Allo-preening was pervasive prior to and leading up to the first contact call produced ( $X = 96$  events per individual,  $\text{SE} \pm 10$  events,  $N = 55$  individuals, 5705 events). Allo-preening began at on average 6.8 days post-hatch ( $\text{SE} \pm 0.6$  days) and occurred at an earlier age

in larger broods (GLMM slope =  $-0.77 \text{ SE} \pm 0.24$ ,  $F_{1,46} = 10.05$ ,  $P < 0.001$ ).

### Brood size and social networks

Sociograms of different brood sizes revealed that nestlings tended to exploit opportunities for preening with available nest mates (Figure 1). Edge densities ranged from 0.86 to 1.00 and increased with brood size (GLMM,  $F_{2,46} = 7.24$ ,  $P < 0.002$ ; Table 1, Figure 1). Hatch order significantly influenced in-strength ( $F = 6.92$ ,  $P < 0.001$ ) (Figure 2b), with earlier hatched individuals being consistently preened by a larger number of actors. AIC analysis indicated two top-ranked models predicting in-strength included out-strength and hatch order ( $w = 0.35$ ) and out-preening duration and hatch order ( $w = 0.31$ ; Table 2). Evidence Ratios (1.07) indicated similar empirical support for the two models, and at least four times the support for any other models included in the set (Table 2). Effect sizes of each factor in the top two models were nearly identical ( $\beta^2 = 0.39$ ,  $f_c = 0.43$ ), CIs did not include zero and both estimates were significant (all  $P < 0.01$ ). Thus, the age hierarchy was enforced by preening older, larger more experienced nest mates.

### Age at first contact call production

All nestlings produced contact calls prior to fledging (20.85 days post hatch  $\pm 1.6$ , Mean  $\pm \text{SE}$ ), though this varied from an average of 17.8 days ( $\pm \text{SE} 1.9$ ) in small broods, to 21.4 ( $\pm \text{SE} 0.5$ ) in medium size broods and to 23.3 ( $\pm \text{SE} 1.4$ ) in large broods (Figure 2a). AIC analysis indicated that full models including out-strength or absolute measures of out-preening, combined with the brood size  $\times$  hatch order interaction, had the highest weights among models predicting age at first contact call production ( $w_i = 0.19 - 0.33$ ) and Evidence Ratios indicated nearly equal empirical support ( $ER = 1.10 - 1.74$ ; Table 3). Out-strength had a medium effect size ( $\beta^2 = 0.58$ ) compared to the relatively small effects of absolute measures of preening ( $\beta^2 = 0.16 - 0.17$ ), its CI did not include zero and the estimate was highly significant ( $P < 0.001$ ; Table 3). Thus, preening in general, and consistently preening more individuals in particular, delays contact call acquisition.

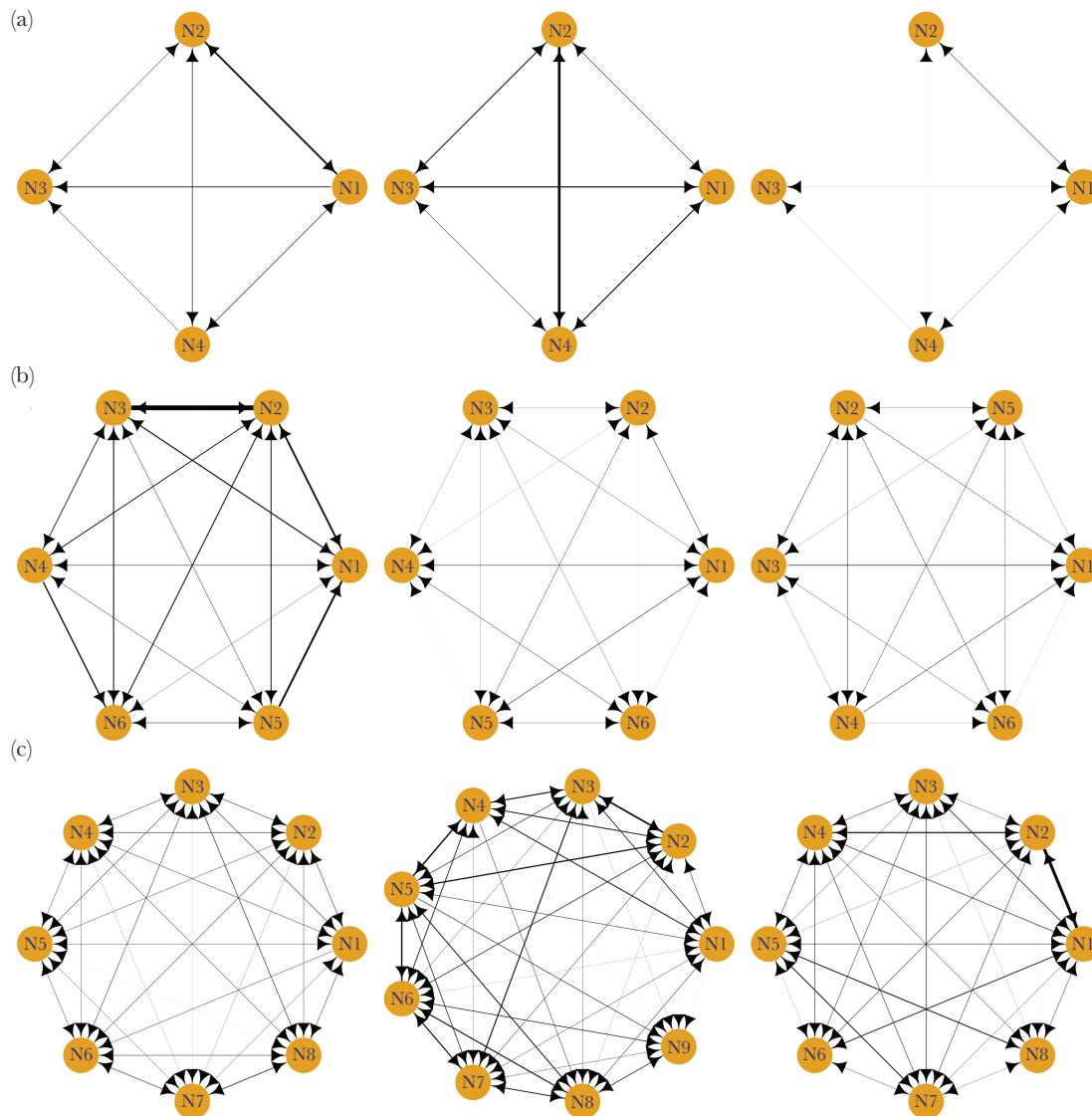
### Social networks and structure of contact calls

QAP correlation tests comparing weighted social network matrices with SPCC matrices did not reveal clear correlations within broods (Supplementary Table S3). One brood of 4 had a contact call similarity matrix that was positively correlated to its weighted social network matrix (QAP,  $R = 0.90$ ,  $P < 0.043$ ), whereas a brood of 6 had an SPCC matrix that was negatively correlated to its social network matrix ( $R = -0.52$ ,  $P < 0.015$ ). The rest were uncorrelated. Given the multiple nonsignificant relationships, these cases did not meet the significance threshold (FDR  $\alpha = 0.0029$ ). Spectrograms of contact call examples from each individual are provided in the Supplementary Material (Supplementary Figure S1).

$k$ -means cluster analysis based on SPCC-MDS showed that parrotlet contact calls could be categorized into eight different structural classes of contact calls (Figure 3A). Larger broods occupied a larger portion of multidimensional acoustic space (Figure 3C-F) and had higher diversity indices in the usage of signal types (Figure 3B).

## DISCUSSION

Parrotlets showed evidence that early social preening delays vocal signature development. While the origins of vocal learning have

**Figure 1**

Weighted bi-directional sociograms based on 2240 allo-preening events in nine broods distributed across three brood sizes: 4 (a), 6 (b), and 8,9 (c). Arrows indicate direction of preening; thickness of edges is weighted by the number of events. Nodes (circles) are labeled according to hatching sequence. Social network degree increased predictably with the number of nodes.

**Table 1****Characteristics of nine nests where allo-preening interactions ( $N = 2240$ ) and age of first contact call were determined**

Nest	Brood		Age	Sex	Degree		Edge		Strength	Age at First call
	Size	Range			In	Out	Density	In	Out	
11B14A	4	7		0.25	2.50	2.50	0.83	0.68	0.52	19.25
13B35A	4	4		0.25	3.00	3.00	1.00	0.55	0.49	20.25
16B30A	4	5		0.25	2.25	2.25	0.75	0.66	0.46	14.00
11B28A	6	7		0.67	4.67	4.67	0.93	0.51	0.47	21.17
11B42A	6	7		0.33	4.50	4.67	0.93	0.61	0.44	22.50
16B36A	6	14		0.5	4.17	4.17	0.83	0.50	0.57	20.67
11B23B	8	11		0.25	6.63	6.63	0.95	0.39	0.46	21.38
14B87A	8	10		0.63	6.88	6.88	0.98	0.77	0.70	22.38
14B23A	9	11		0.67	7.33	7.33	0.92	0.62	0.54	26.11

Brood refers to number of nestlings per brood; Age Range is age range of each brood in days post-hatching; Degree refers to mean number of directional relationships; Strength refers to mean number of partners weighted by the number of interactions; Edge Density refers to the mean portion of relationships exhibited out of all possible relationships; Age Onset Adj. refers to the Age Onset as proportion of the fledging age.

**Table 2**

**Top models (95% confidence subset) predicting in-strength based on 2240 preening events in nine broods. Brood identity was included as a random effect in each model. For each factor in each model, effect size and 95% confidence intervals (CI) are provided. Complete model sets are provided in Supplementary Table S1**

Model	k	AICc	$\Delta\text{AICc}$	$w_i$	ER	Factor	Effect	95% CI			
								Lower	Upper	#	
I	7	11.84	0.00	0.35		Out-strength	0.393	0.282	0.646	#	**
						Hatch	0.432	0.294	0.569	#	***
II	7	12.11	0.27	0.31	1.07	Out-preen dur	0.387	0.279	0.630	#	***
						Hatch	0.429	0.292	0.566	#	***
III	8	14.84	3.00	0.08	4.20	Sex	0.210	-0.321	0.741	*	**
						Hatch	0.419	0.283	0.555	#	**
IV	7	14.85	3.01	0.08	4.22	Out-preen freq	0.322	0.243	0.474	#	*
						Hatch	0.433	0.295	0.570	#	**
V	10	15.35	3.51	0.06	5.42	Out-strength	0.394	0.283	0.650	#	**
						Brood	0.123	-0.076	0.322	#	***
VI	10	15.59	3.75	0.05	6.11	Hatch	0.419	0.283	0.555	#	***
						Out-preen dur	0.388	0.280	0.635	#	**
VII	7	18.34	6.50	0.01	24.17	Brood	0.124	-0.075	0.323		***
						Hatch	0.417	0.281	0.553		
						Sex ratio	0.179	0.152	0.218	#	*
						Hatch	0.362	0.231	0.492	#	*

*k* is the number of parameters estimated. AIC = Akaike Information Criteria scores corrected for small samples sizes; *w* = AIC weights; ER = Evidence Ratio; # = CI does not include zero; \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ .

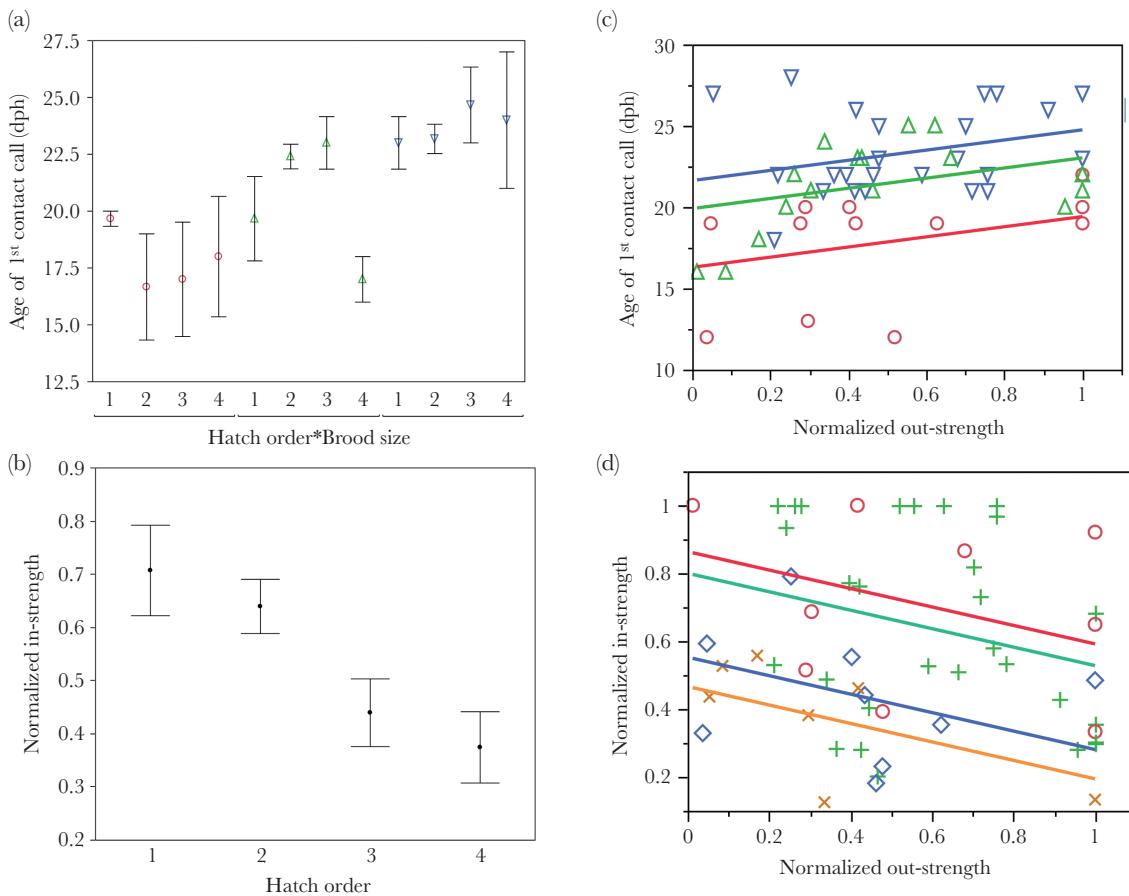
inspired much debate, there is general agreement that ontogeny can provide insights into evolutionary processes and that vocal learning does not develop *de novo* but develops late in maturation as part of a broader system of social learning. Development often proceeds by co-opting preexisting motor, cognitive and perceptual systems that served different purposes at earlier stages in development (Feenders et al. 2008; Nottebohm and Liu 2010; Syal and Finlay 2011; Kingsley et al. 2018). Our study showed that preening was widespread and occurred well before the first contact call; parrotlets indicated a proclivity to preen as many social companions as brood size permitted; and involved coordinated bill and tongue movements in an intimate and unambiguous social context. While experimentation is necessary to confirm causes and consequences of delayed maturation, allo-preening is a candidate for understanding of how social motivation and age hierarchy influence the transition between innate vocal signals and the onset to vocal learning.

### Social preening behavior

Parrotlets demonstrated that allo-preening, an important adult social behavior, has its early beginnings during cryptic sibling interactions inside the nest cavity. In many animals the early socialization process involves learning to navigate relationships with adult caregivers and close kin. Birds have provided a wealth of information on early sibling interactions (Wright and Leonard 2007). Most studies have focused on the competitive effects of begging behavior, usually during brief feeding sessions with adults. In altricial birds, adults are often absent as they search for food, so siblings spend more time with each other than they do with adults, yet the consequences of these interim periods have received less attention (Stöwe et al. 2008; Dreiss et al. 2014; Ducouret et al. 2020).

Our study showed that when adults are absent other non-competitive and socio-positive behaviors prevail. While experimentation is needed (e.g., de-parasitization, cross-fostering, hormone supplements, etc.), sibling allo-preening behavior reported on here satisfies the requirements of social play (Graham and Burghardt 2010), an important correlate of avian cognition (Ricklefs 2004). Nestling allo-preening is: (1) lackadaisical and incomplete in a functional sense, and (2) less serious from the reproductive context in which adult pairs preen each other or their offspring (Waltman and Beissinger 1992); (3) it appears spontaneous, voluntary and recipients rarely refuse overtures, suggesting that out- and in-preening are both appealing; (4) it is repeated across different, and without help, hard-to-reach body regions (e.g., head and neck) and feather types (i.e., contour, remiges, and retrices), and thus not performed in a stereotypic manner (Supplementary Movie 1); (5) play behaviors are also thought to be initiated in the absence of severe stress (Graham and Burghardt 2010), and can even reduce stress (Stöwe et al. 2008). Parrotlet nestlings in this population are not on average chronically stressed (Berg et al. 2019) and the fact that 99% of nestlings in this study fledged successfully, adds further evidence that most participants allo-preened in lieu of severe stress. Allo-preening is thus a formative part of social play in developing parrotlets and perhaps in other parrots, or in other altricial cavity-nesting birds (e.g., Strigiformes: owls; Piciformes: woodpeckers and toucans; Apodidae: swifts) (Van Tyne 1929; Weathers et al. 1990; Ducouret et al. 2020).

Interestingly, out-strength was inversely correlated with in-strength (Figure 2d), even after controlling for hatch order and brood identity, suggesting that social preening might be better

**Figure 2**

Diversity of allo-preening interactions delays the first contact call. (a) Mean ( $\pm$ SE) age at first contact call as a function of hatching sequence and brood size. (b) Mean in-strength as a function of hatching sequence. (c) Age at first contact call as a function of out-strength, controlling for brood size. Lines and symbols are color-coded for brood sizes (red circle = 4, green triangle = 6, blue inverted triangle = 8–9). (d) In-strength as a function out-strength controlling for hatch sequence (red circle = 1, green plus = 2, blue diamond = 3, orange x = 4).

viewed as a commodity that can be traded (Noë and Hammerstein 1995; Ducouret et al. 2020)—social preening might be a negotiation tactic by younger siblings to motivate reciprocal behavior in older, larger more experienced nest mates. Because all were close kin, reciprocating behavior may be compensated via indirect and direct benefits. However, understanding this will require more work.

### Social networks

Our study indicated that the number of individuals preened to be as or more important to ontogenetic scheduling than the absolute amount of preening. Out-strength and absolute measures of preening were highly correlated (all  $R > 0.92$ ), however, we should not conclude that they are synonymous. Our study indicates that the only way to achieve a large amount of time spent preening is by increasing the number of social companions. Most studies that address effects of social complexity on behavior in free-ranging animals use Gambit of the Group, which assumes that all individuals observed in close proximity to one another as being associated with each other (Farine and Whitehead 2015). While relevant in many ecological contexts (e.g., mosquito-borne pathogen transmission), subtle aspects of social cognition are often influenced by the number of direct social bonds rather than group size per se. We quantified intimate, tactile interactions in wild nestlings, which revealed that nestlings do not necessarily preen with all other nestlings equally over the course of the nestling period, despite being

in immediate proximity and in a closed network. We found some evidence of age-hierarchical ordering of network topology in larger broods and top ranked models included hatch order and out-strength predicting in-strength. However, small, closed, nearly complete networks limited more in-depth analysis. Social network analysis in behavioral ecology usually involves searching for topological and structural patterns across many individuals and has less often been concerned with comparing structure across a large number of unconnected networks. Our study was admittedly different in the large number of small, closed networks. Given the possibility of random interactions, our results should be viewed with caution (Supplementary Table S1). Nonetheless, the random effects, intercept only model ranked last in an exhaustive AIC analysis (Supplementary Table S3); brood sizes used are relevant to early social environments in nature, and nestlings actively exploited opportunities for social interactions with nest mates of markedly different ages and experience levels, processes which resulted in an exponential increase in the number of directional relationships as brood size increases (Figure 1). Thus, brood size, the age hierarchy and socially motivated allo-preening conspired to produce significant variation in early social environment.

### Allo-preening and age of first contact call

The number of favored preening partners postponed a developmental milestone in a socially acquired trait. Out-strength was

**Table 3**

**Top models (95% confidence set) predicting age at first contact call based on 2240 bi-directional allo-preening events in nine broods.** Brood identity was included as a random effect in each model. For each factor in each model, effect sizes and 95% confidence intervals (CI) are provided. Complete model sets are provided in [Supplementary Table S2](#)

Model	k	AICc	$\Delta\text{AICc}$	$w_i$	ER	Factor	Effect	95% CI			
								Lower	Upper	#	**
I	15	199.08	0.00	0.33	1.10	Out-strength	0.56	0.358	1.263	#	**
						Brood	0.28	0.072	0.481	#	*
						Hatch	0.14	0.023	0.252	#	
						Brood $\times$ Hatch	0.37	0.302	0.442	#	
II	15	199.31	0.23	0.30	1.10	Out-preen Dur	0.17	0.146	0.206	#	*
						Brood	0.28	0.072	0.481	#	*
						Hatch	0.14	0.022	0.251	#	
						Brood $\times$ Hatch	0.38	0.305	0.446	#	
III	15	200.16	1.08	0.19	1.74	Out-preen freq	0.16	0.134	0.184	#	*
						Brood	0.26	0.058	0.465	#	*
						Hatch	0.14	0.030	0.259	#	
						Brood $\times$ Hatch	0.36	0.293	0.428	#	*
IV	15	201.75	2.67	0.09	3.67	Sex ratio	-0.02	-0.023	-0.022		
						Brood	0.18	-0.016	0.386		
						Hatch	0.09	-0.024	0.201		
						Brood $\times$ Hatch	0.38	0.308	0.450	#	**
V	15	204.93	5.85	0.02	16.50	In-strength	-0.01	-0.008	-0.008		
						Brood	0.27	0.065	0.474	#	*
						Hatch	0.06	-0.050	0.174		
						Brood $\times$ Hatch	0.45	0.363	0.531	#	*
VI	15	205.08	6.00	0.02	16.50	In-preen Dur	-0.01	-0.013	-0.013		
						Brood	0.27	0.066	0.474	#	
						Hatch	0.07	-0.047	0.178		
						Brood $\times$ Hatch	0.44	0.361	0.528	#	

AICc = Akaike Information Criteria corrected for small sample sizes; k = number of parameters; ER = Evidence Ratio; # = CI does not include zero; \* =  $P < 0.01$ , \*\* =  $P < 0.001$

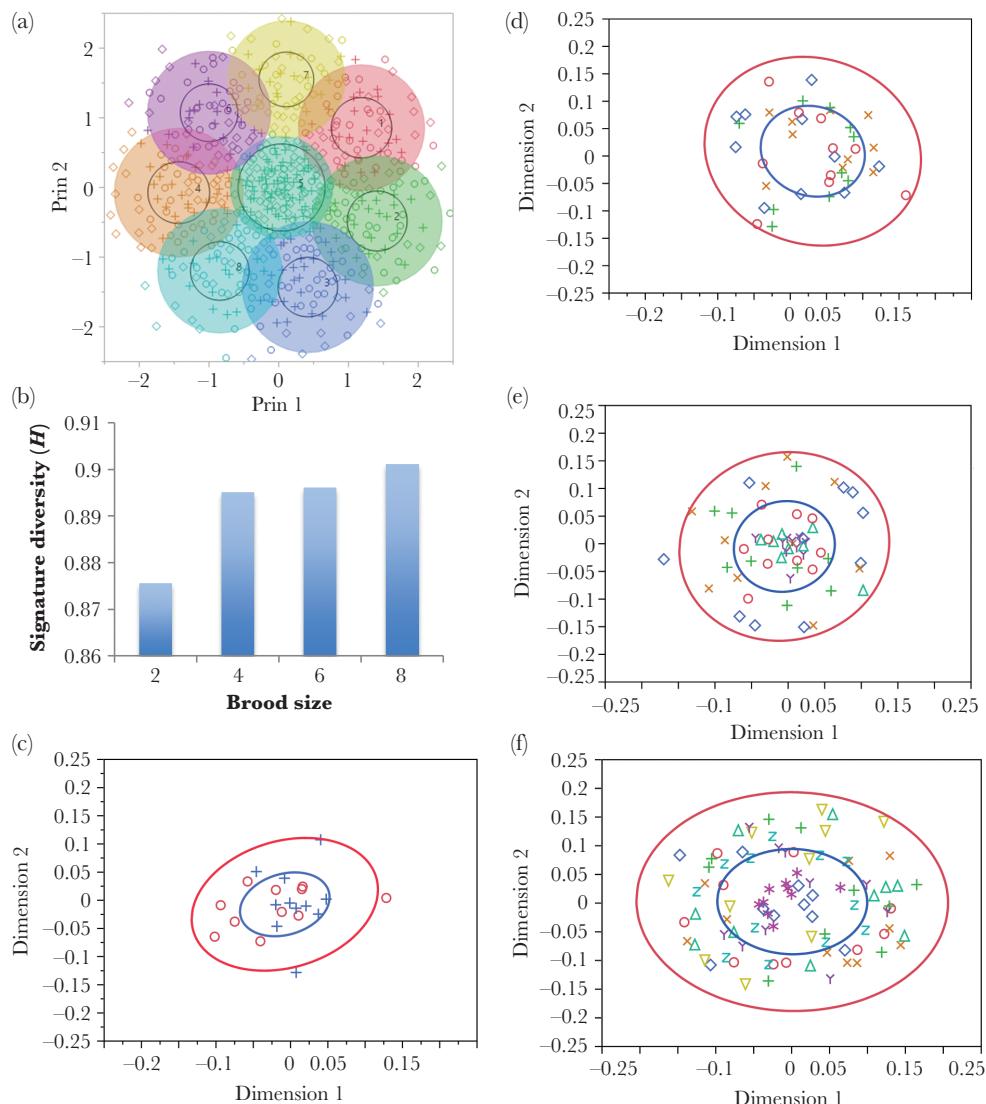
positively related to age at first signature contact call (Figure 2C), even after controlling for repeated measures within broods; limitations imposed by brood size and independently of delayed growth in later-hatched individuals (Stoleson and Beissinger 1997). While brood, call-playback or endocrine manipulation experiments are required to understand the precise sensitive periods and causal scenarios involved, results suggest that the window for learning of vocal signatures is vulnerable to the diversity of upstream social interactions. In birds and mammals, exploratory social behaviors delay maturation in hierarchically ordered brain regions through a neural pruning process that tailors to prevailing social contexts (Ferdman et al. 2007). Because preening involves bill and tongue movements, our evidence showing a delay in late-developing contact calls could be the result of a diversity of differentiated preening relationships inducing differential pruning on vocal production learning circuits in parrotlet brains. However, social influences on the development of brain neuro-anatomy in parrots has received less attention compared to the more popular songbird models (Heaton and Brauth 2000; Brauth et al. 2006; Charvet and Striedter 2008). Little is known about how social-motivational and vocal production learning circuits become integrated in nature, but is relevant to understanding the adaptive function of evolutionary-developmental departures (Nottetbohm and Liu 2010; Syal and Finlay 2011; Baran et al. 2017)

A non-mutually exclusive explanation is that formation of a unique signature call might become computationally challenging in larger broods. For example, the second hatched individual in a brood of two might be better able to select structural-acoustic attributes that differ from its older sibling, permitting individual recognition by parents. Whereas the eighth-hatched nestling in a large

brood might need more time to sort-out the diversity of its seven older siblings' calls to which it has already been exposed. This is consistent with a large literature on the effects of social complexity on signal complexity (Social Complexity Hypothesis) (Freeberg et al. 2012; Bergman and Beehner 2015), but would benefit from brood size manipulations, work underway.

### Contact calls and vocal diversity

Our result of contact call diversity increasing with brood size (Figure 3) is consistent with social complexity as a driver of signal complexity, which has less often been concerned with early developmental processes. Parrotlets began making their first contact calls on average 21 days post-hatching, corroborating previous estimates (Berg et al. 2013), and usually weeks after they began tactile social interactions. Comparisons between weighted social network matrices and contact call similarity matrices indicated that parrotlets do not on average converge on attributes of call structure with favored preening partners, but rather each individual developed its own unique call (Supplementary Figure S1; Supplementary Table S3). Our result of a significant effect of hatch order on in-strength indicates hierarchical influences of preening are related to the hierarchical emergence of contact calls. As a result, signature calls in larger broods collectively tended to occupy larger portions of multi-dimensional acoustic space and had higher repertoire diversity as a group. Thus, larger broods collectively produced more vocal diversity as a result of allo-preening's enforcement of the hierarchy and its effects on vocal signature acquisition dates. While we still cannot yet say how signature attributes arise, results indicate that the staggering of contact call acquisition dates, and likely staggering of

**Figure 3**

Multi-dimensional Scaling (MDS) based on Spectrographic Cross-Correlation (SPCC) of 586 contact calls from 59 nestlings distributed across 11 broods of green-rumped parrotlet nestlings. (a) k-means cluster analysis identified 8 clusters representing different signal types. (b) Larger broods had higher mean Shannon-Wiener Diversity scores indicating that larger broods tended to use a larger number of signal types. SPCC-MDS dimension plots of contact calls from one brood of each size (c) 2, (d) 4, (e) 6, and (f) 9 nestlings. Density ellipses are for 95 and 50% confidence intervals. Individuals are indicated by unique symbols.

auditory learning periods, likely contributed to signature call formation and vocal diversity.

### Allo-preening and allo-grooming

Parrotlets that preened a relatively large number of siblings postponed their development of vocal signature learning. Allo-grooming in primates is intimately related to contact calls especially in larger more dispersed groups and has been suggested to have eventually led to imitation of vocal signatures as a way of engaging social companions in large human groups (McComb and Semple 2005; Arlet et al. 2015; Kulahci et al. 2015; Dunbar 2017). Mammals and vocal learning birds, despite being separated by over 300 million years from a common ancestor, converged on similar gene expression patterns in late-developing brain regions that control vocal imitation (Pfenning et al. 2014), however, the behavioral modifications and ecological sources of selection that led

to convergence in mammals and birds are still the subject of debate (Fitch et al. 2010; Nowicki and Searcy 2014). In parrotlets, allo-preening's downstream effects on the onset to vocal signature learning and links to vocal diversity could point to a potentially convergent scenario with allo-grooming's role in the evolution of complex social communication.

### Conclusion

A well-known example of allo-grooming's role in the evolution of complex mammalian communication has a potential analogue in allo-preening networks and vocal production learning during early development in a wild bird. Affiliative social behaviors can play an important epigenetic role in shaping cognitive phenotypes in many species (Duckworth 2015; Sapolsky 2017). In highly social parrotlets we found the diversity of preening networks to be especially important in ontogenetic scheduling of a cognitive trait, however,

we cannot rule-out more immediate benefits: ectoparasite removal during allo-preening could directly aid hygiene; out-preening might involve repeated assaults on gastrointestinal microbiomes, with potential effects on nutritional state (Pacheco et al. 2004), immune and or cognitive function (Carlson et al. 2018). Sibling preening in general may ameliorate adverse effects of stress (Stöwe et al. 2008), reducing allostatic load during critical periods of growth and maturation (Romero and Wingfield 2016; Berg et al. 2019). Because adult caregivers initially perform preening and feeding of neonates, siblings may contribute to parental and personal fitness by partially assuming allo-parenting responsibilities of siblings, while building social skills that allow flexibility in navigating adult social networks.

## SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

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