



Parent–environmental interactions shape acoustic signatures in tree swallows: a cross-fostering experiment

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Acoustic signatures are common components of avian vocalizations and are important for the recognition of individuals and groups. The proximate mechanisms by which these signatures develop are poorly understood, however. The development of acoustic signatures in nestling birds is of particular interest, because high rates of extra-pair paternity or egg dumping can cause nestlings to be unrelated to at least one of the adults that are caring for them. In such cases, nestlings might conceal their genetic origins, by developing acoustic signatures through environmental rather than genetic mechanisms. In a cross-fostering experiment with tree swallows *Tachycineta bicolor*, we investigated whether brood signatures of nestlings that were about to fledge were attributable to their genetic/maternal origins or to their rearing environment. We found that the calls of cross-fostered nestlings did not vary based on their genetic/maternal origin, but did show some variation based on their rearing environment. Control nestlings that were not swapped, however, showed stronger brood signatures than either experimental group, suggesting that acoustic signatures develop through an interaction between rearing environment and genetic/maternal effects.

Many social interactions rely on acoustic signals that carry signatures of individual identity or group membership. Acoustic signatures have been demonstrated across a wide variety of species (Stevenson et al. 1970, Mammen and Nowicki 1981, Hile et al. 2000, Lovell and Lein 2005, Sharp et al. 2005, Vignal et al. 2008, Jacot et al. 2010). Nonetheless, they are thought to be particularly characteristic of avian calls and songs, notably those used to cooperate with particular social partners (Price 1999, Sharp and Hatchwell 2006), to direct care to offspring rather than unrelated young (Aubin and Jouventin 2002), or to discriminate established territorial neighbours from new rivals (Radford 2005).

Despite their prevalence in avian vocalizations, surprisingly little is known about how acoustic signatures develop. The distinctiveness required for acoustic signatures may already be provided by each individual's unique genotype and developmental history (Forstmeier et al. 2009). Selection may, however, favour adaptive changes to inheritance or ontogeny that enhance distinctiveness, if advertising identity or group membership is particularly advantageous. Conversely, mechanisms that suppress distinctiveness might evolve, if such advertising is deleterious. Note that here we use the term 'acoustic signature' for any case in which acoustic signals are distinctive and specify 'adaptive acoustic signature' if the distinctiveness is used by receivers and is thus beneficial for the sender.

An especially well-understood signal that is particularly amenable to developmental studies is the begging call of nestlings. A few studies have shown that begging calls differ between individual nestlings, especially late in the nestling period, when calls are usually more complex and stereotyped (Brittan-Powell et al. 1997, Leonard et al. 1997a). In general, parents tend not to use this individual variation to discriminate amongst nestlings and simply feed any nestlings that are in their nest, even though they do use other sources of call variation to distribute feedings (Leonard and Horn 2001a). The exceptions appear to be in bird species that engage in brood division, where adults use individually distinct calls to direct care to their own subset of offspring (Draganoiu et al. 2006). Similarly, in colonial species where young from different broods mix after fledging, parents also use the calls to direct feedings to their own offspring (Medvin et al. 1992).

It is often not clear, even in cases where discrimination occurs, if acoustic signatures are favoured by natural selection or are simply by-products of individual variation that parents use. More convincing evidence for adaptive acoustic signatures comes from species in which brood mates share similar begging calls, suggesting that the calls serve to advertise brood membership to parents. The best such evidence for evolved brood signatures comes from comparative studies of swallows, in which both the distinctiveness

of signatures and the strength of their discrimination by parents increases with coloniality and thus with the likelihood that young from different broods intermingle (Medvin et al. 1992, 1993).

Apparently adaptive brood signatures of this kind potentially develop via two, non-mutually exclusive, developmental mechanisms (Komdeur and Hatchwell 1999). The simplest mechanism, at first glance, is that signatures are shaped by genetic or maternal effects (common origin), so that individuals within the same brood share a signature because they are genetically related. Whether such a mechanism would evolve in birds, however, is complicated by the frequent occurrence of brood parasitism or extra-pair paternity. In such cases, the unrelated offspring may be selected to suppress their distinctiveness from their host brood mates, so that they can extract care from the attending parents (Beecher 1991, Johnstone 1997, Pagel 1997).

A second potential developmental mechanism for brood signatures is that they are shaped by environmental effects (common environment), and therefore shared by individuals that have the same living conditions or social interactions. Nestlings could, for example, modify their calls to sound more similar to their brood mates' calls, either to suppress their genetic origins as described above, or to conform to the call structure that best elicits care from parents. Of course, signatures may develop through a combination of both genetic and environmental factors, depending on the relative benefits of distinctiveness versus conformity, as well as developmental constraints.

Cross-fostering experiments with young birds provide some evidence for a genetic/maternal basis to call structure, suggesting that brood signatures could have a common origin. In young cliff swallows *Hirundo pyrrhonota*, for instance, the time-frequency patterning of begging calls appears to be genetically based (Medvin et al. 1992). Similarly, in nestling great tits *Parus major* call amplitude is mainly explained by brood of origin and not rearing (Kölliker et al. 2000). Evidence also exists, however, for an environmental effect. For example, in long-tailed tits *Aegithalos caudatus* (Sharp et al. 2005, Sharp and Hatchwell 2006) and green-rumped parrotlets *Forpus passerinus* (Berg et al. 2012) siblings learn common contact calls from care-giving adults. Similarly, in both barn owls *Tyto alba* (Roulin et al. 2009, Dreiss et al. 2010) and tree swallows *Tachycineta bicolor* (Leonard et al. 2009), the structure of nestling begging calls converge when nestlings call together. While this call convergence has not been directly linked to call development, it does show that social interactions with brood mates influence call structure. Together, the few studies that have been conducted to date suggest nestling brood signatures might have genetic/maternal, environmental, or mixed origins.

Here, we use a cross-fostering experiment to determine whether brood signatures in nestling tree swallows are based on genetic/maternal effects, environmental effects, or both. Tree swallows are ideal models for examining these questions, because they breed in loose colonies, where offspring from different broods mix after fledging and so are expected to have some mechanisms such as brood signatures for identifying young after fledging (Leonard et al. 1997a). Indeed, previous work has shown that siblings have call

durations and frequencies that are more similar than non-siblings, suggesting that these call features could provide a brood signature (Leonard et al. 1997a). At the same time, however, rates of extra-pair fertilization are very high in most populations. Up to 69% of nestlings can be extra-pair and up to 87% of broods can have extra-pair young (Kempnaers et al. 2001, Barber et al. 2005). So nestlings might benefit from suppressing their genetic origins. Based on these pieces of evidence, we would predict a greater role of rearing environment than origin in call development.

Methods

We conducted this study in the Gaspereau Valley of Nova Scotia, Canada (45°4.5'N, 64°20.0'W) between May and July 2010 using a population of tree swallows nesting in nestboxes (study site described in detail in Leonard and Horn 1996). Nestling age was determined by checking nestboxes daily around the anticipated hatching date (hatch day = day 1). To account for potential differences in begging call structure between sexes, we took a small blood sample (approximately 5 µl) from the brachial vein of each nestling on day 13 and used the P2/P8 primer method (Griffiths et al. 1998) to molecularly determine the sex of nestlings.

Cross-fostering and recording

We used a total of 18 nests: six control nests and 12 (four groups of three nests) cross-fostered nests. Control nests and cross-foster nests did not differ in laying date (19–26 May 2010), clutch size (student's *t*-test: mean ± SD 6.0 ± 0.6 and 5.7 ± 1.4, *p* = 0.35) or brood size (student's *t*-test: mean ± SD 5.3 ± 0.8 and 5.2 ± 0.7, *p* = 0.79). We matched cross-fostered broods for age, size and proximity and at 3–4 d of age (maximum of one day difference amongst broods) cross-fostered nestlings using a nonreciprocal design, with nestlings swapped across a triplet of nests so that all nestlings were reared in a foster nest (i.e. nestlings from nest A were divided between nests B and C, nestlings from nest B were divided between C and A and so on, Fig. 1; Mateo and Holmes 2004). This design allowed us to separate genetic/maternal effects from environmental effects, because no nestling grew up in its home nest (Kölliker et al. 2000, Mateo and Holmes 2004). Because of the high rates of extra-pair paternity in this species, our experiment addressed genetic/maternal effects from the female parent, but was unlikely to provide a strong test of effects from the male parent.

To balance nestling size across cross-fostered nests, we ranked nestlings by weight in their home nest and then transferred them to foster nests based on those ranks (i.e. heaviest nestling of nest A moved to nest B, second heaviest moved to nest C, third heaviest to nest B, and so on). Within each triplet, all nestlings were marked with a unique colour combination indicating their brood of origin and individual identity by dyeing their toes with permanent non-toxic marking pens. Nestlings from control nests received the identical treatment, apart from a move to another nest.

To verify that the nestling tree swallows in this study showed brood signatures, and to determine whether call

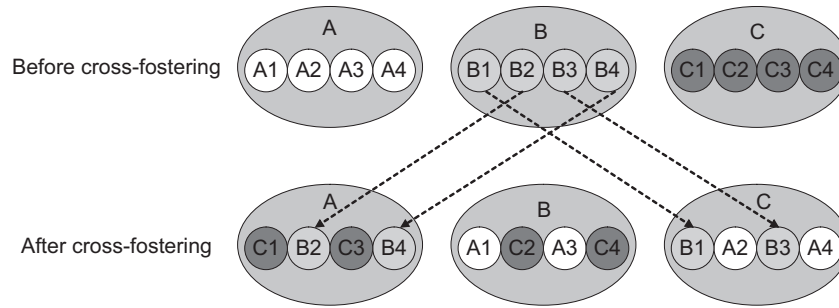


Figure 1. Nonreciprocal cross-fostering design. All nestlings grow up in foster nests. Nestlings are ranked by weight and distributed to foster nests alternately (i.e. heaviest nestling of nest A swapped to nest B, second heaviest to nest C, third heaviest to nest B, and so on).

structure was influenced by genetic/maternal effects or environmental effects, we recorded begging calls as individual nestlings sat in the entrance of the nest box a few days before fledging (18–21 d), by which time brood signatures should have developed (Medvin et al. 1993). We placed a shotgun microphone, connected to a solid state recorder and mounted on a tripod, approximately 1.5–2 m from the nestbox. The microphone was beneath the nest box and at an approximately 45° angle, facing the front of the nestbox. To identify nestlings from a distance, we individually marked each nestling by dyeing the white throat feathers on day 13, using the same colours as used on the toes. This enabled us to identify the individual occupying the entrance of the nestbox from 30–40 m distance using a spotting scope.

Sound analysis

We recorded begging calls of 22 nestlings at the six control nests and 38 nestlings at 10 of the 12 cross-fostered nests (see Fig. 2 for examples). Two cross-fostered nests were depredated, one each from a different triplet. However, because of the nonreciprocal cross-fostering design, at least some nestlings from each of the 12 broods of origin were

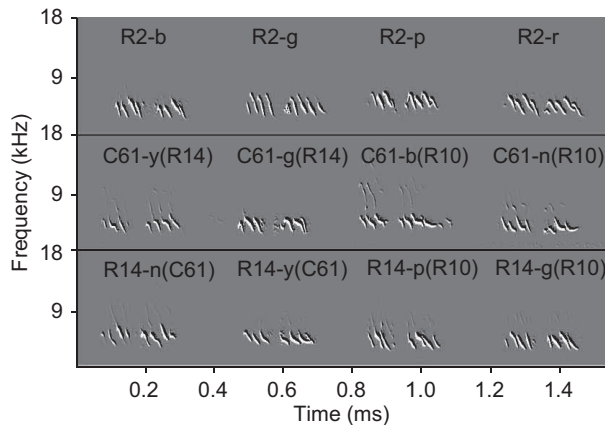


Figure 2. Spectrograms of the calls of four tree swallow nestlings from a control brood (upper row) and two cross-fostered broods (lower two rows). Labels indicate the nest of origin (e.g. ‘R2’), individual nestling (e.g. ‘-b’), and, in brackets for cross-fostered nestlings only, foster nest (e.g. ‘(R14)’). Broods depicted here were chosen at random from broods of four nestlings.

recorded. We used Sound Analysis Pro (SAP) (for details see Tchernichovski et al. 2000, Tchernichovski and Mitra 2004) to measure the following nine call features (see Table 1 for descriptions) of the first 25 calls on each recording that were free of background noise (total of 610 calls from 60 nestlings, mean \pm SD 10.2 ± 5.8 calls/nestling, range: 1–25 calls/nestling): 1) duration of call part (in ms); 2) variance of amplitude modulation (in ms^{-1}); 3) mean frequency (in Hz); 4) mean frequency modulation ($^\circ$); 5) variance of frequency modulation ($^\circ$); 6) mean entropy; 7) variance in entropy; 8) mean pitch (in Hz) and 9) mean pitch goodness. These features have been previously shown to be important in acoustic signatures, showing considerable variation across songbird nestlings (Jacot et al. 2010, Reers and Jacot 2011, Reers et al. 2011).

Statistical analyses

All statistical analyses were performed with R ver. 2.10.1. Before analysis, all acoustic parameters were Box–Cox-transformed to approach normality by using the R package *car* (Fox 2002). In general, call features were not strongly correlated and, therefore, not considered redundant (mean correlation coefficient = 0.21, range: 0.02–0.73, Table 2), so all were included in the analyses. The analyses described below included automated tests for multicollinearity in the data, and none was detected (package: MASS, Venables and Ripley 2002).

Brood signatures

To test whether broods could be distinguished based on their calls, we used a discriminant function analysis (DFA) (package: MASS, Venables and Ripley 2002). We used the average value for each call feature/nestling to avoid the pseudoreplication that would result from using multiple calls from the same individuals (Mundry and Sommer 2007). In addition to the standard DFA we also calculated a cross-validated (leave-one-out) DFA. In this procedure, the DFA is calculated with one datum (in this case, a nestling) removed, the ability of the resulting DFA to correctly classify is tested with the removed datum, and this process is repeated for every datum. The purpose of the cross-validated DFA is to avoid the circularity of measuring how well nestling calls can be assigned to their broods using the same data used to distinguish broods. The cross-validated DFA is more reliable and conservative, and we base our

Table 1. Tree swallow begging call features. Variance in call features is a measure of change over the duration of the call. High variance indicates relatively large changes, while low variance indicates relatively small changes (for details see Tchernichovski et al. 2000, Tchernichovski and Mitra 2004).

Call feature		Description
Duration (ms)		length of call
Amplitude modulation (ms^{-1})	variance	how widely amplitude changes over time
Frequency (Hz)	mean	average of all frequencies, weighted by their amplitudes
Frequency modulation ($^{\circ}$)	mean	slope of frequency traces, relative to horizontal
Frequency modulation ($^{\circ}$)	variance	variation in frequency modulation over time
Pitch (Hz)	mean	fundamental frequency, calculated from all frequencies weighted by their pitch goodness
Pitch goodness	mean	strength of periodicity in the signal (i.e. how strongly it conforms to its fundamental frequency)
Entropy	mean	noisiness of the signal
Entropy	variance	variation in entropy across the signal

conclusions on its results. Because the standard DFA is more directly based on the data as they were collected, however, we provide the results of that analysis as well.

We first used a DFA to test whether nestlings in control broods could be correctly assigned to a brood based on their call features (mean \pm SD 3.7 ± 1.4 nestlings/nest, range 2–6). Then, to determine if brood signatures were influenced by genetic/maternal effects or environmental effects, we used a DFA to examine whether nestlings from the same home brood, but reared apart ($n = 38$ nestlings from 12 broods of origin) were more likely to be assigned to the same brood, suggesting that brood signatures were due to common origin. In a second set of DFAs, we examined whether unrelated foster nestlings ($n = 38$ nestlings from 10 rearing nests) would be assigned to their nest of rearing, which would suggest that brood signatures were due to common environment. Note that only eleven, rather than twelve, broods of origin were used in the cross-validated DFA for this analysis (which requires at least two samples per group), because only one nestling from one brood of origin survived due to predation.

Variance components of call features

To determine what proportion of the variation in each call feature is explained by differences between broods and therefore could contribute to brood signatures, we analysed the calls of control broods using nine generalized linear mixed effects models (GLMMs; model details below), i.e. one for each call feature. We then used a second set of GLMMs on the call features of nestlings from cross-fostered broods, to determine what proportion of the variation in

each call feature is explained by nestling identity, the common origin of nestlings or the common rearing environment.

For each GLMM we used sex as a fixed factor to account for potential sex differences in call features. This factor was treated as fixed because all possible levels (male, female) were represented in the data. As random effects we used individual identity and brood identity for control nests or individual identity and both nest of rearing and brood of origin for cross-fostered nests, respectively. These effects were treated as random because the individuals and broods represented in the data were only a sample of all possible tree swallow broods. We initially included nestling weight and wing cord length on day 13 in the variance component analysis, however, neither of those morphometric measurements had a significant influence on the analyses and were therefore excluded in the final model. Because all data was Box–Cox-transformed to approach normality we used a normal link function. To quantify the significance of a random effect in contributing to a model, we performed ANOVAs on the complete model compared to a model lacking the random effect of interest.

Results

Brood signatures and call features in control broods

All nestlings from control broods were correctly assigned to their broods using a standard DFA (standard DFA: 100.0% versus 16.7% expected by chance; binomial test, $p < 0.001$; $n = 22$ nestlings from six nests). In the

Table 2. Pearson correlations between individual acoustic parameters, bold typing indicates significant correlations (610 calls from 60 nestlings, significance level of $p < 0.05$).

		Duration (ms)	Amplitude modulation (ms^{-1}) variance	Frequency (Hz) mean	Frequency modulation mean	Frequency modulation variance	Entropy mean	Entropy variance	Pitch (Hz) mean
Duration (ms)									
Amplitude modulation (ms^{-1})	variance	-0.29							
Frequency (Hz)	mean	0.13	-0.07						
Frequency modulation	mean	0.04	0.10	0.33					
Frequency modulation	variance	-0.03	-0.09	-0.15	-0.44				
Entropy	mean	-0.21	0.21	0.18	-0.07	-0.05			
Entropy	variance	-0.19	0.08	-0.33	-0.02	0.11	-0.13		
Pitch (Hz)	mean	0.17	-0.03	0.73	0.64	-0.12	-0.03	-0.28	
Pitch goodness	mean	-0.09	0.18	0.22	0.37	-0.11	0.67	-0.32	0.40

cross-validated DFA, 12 nestlings were assigned to their correct nest of rearing, which is significantly more than expected by chance (cross-validated DFA: 54.5% versus 16.7%, binomial test, $p < 0.001$; $n = 22$ nestlings from six nests). This suggests the existence of a common brood signature among siblings.

The variance components analysis revealed that brood identity contributed significantly to the variation in call duration, variance in amplitude modulation, mean frequency, mean entropy, variance in frequency modulation and mean pitch, but not mean frequency modulation, variance of entropy or mean pitch goodness (Table 3).

Brood signatures and call features in cross-fostered nestlings

Genetic/maternal effects

Twenty-six of 37 nestlings that were originally brood mates, but were reared in different nests, were assigned to their correct brood of origin (common origin), which is significantly more often than expected by chance (standard DFA: 70.3% correct assignment versus 9.1%; binomial test, $p < 0.001$, $n = 37$ nestlings from 11 rearing nests). In the cross-validated DFA, four of the 37 nestlings were assigned to their correct brood of origin, which did not differ significantly from chance (cross-validated DFA: 10.8% correct assignment versus 9.1%; binomial test, $p = 0.58$, $n = 37$ nestlings from 11 rearing nests).

The variance component analysis revealed that brood of origin did not contribute significantly to the variation in any of the call variables (Table 3).

Environmental effects

Twenty-eight of 38 nestlings that were reared together but originated in different nests, were assigned to their correct brood of rearing (common environment), which is significantly more often than expected by chance (standard DFA: 73.7% correct assignment versus 10.0%; binomial test, $p < 0.001$, $n = 38$ nestlings from 10 rearing nests). In the cross-validated DFA, eight of the 38 nestlings were assigned to their correct brood of rearing, an assignment rate that was marginally non-significant (cross-validated DFA: 21.1% correct assignment versus 10.0%; binomial test, $p = 0.051$, $n = 38$ nestlings from 10 rearing nests).

The variance component analysis showed that brood of rearing contributed significantly to the variation in call duration and variance of entropy (the variability in the noisiness of each call) (Table 3).

Discussion

Our results for control broods confirm evidence from a previous study for brood signatures in tree swallows (Leonard et al. 1997a) and suggest that a number of call features could contribute to the brood signature. We found no evidence for genetic/maternal effects in our call analyses on cross-fostered broods and the cross-validated DFA did not assign nestlings to their correct nest of origin. We found evidence for a weak effect of the rearing environment, with two call features significantly affected by rearing environment, however, correct assignment rate in the cross-validated DFA was not significant (albeit marginally so). Thus brood signatures in this species show neither genetic/maternal nor environmental effects alone, but instead appear to develop through an interaction between a nestling's genetic/maternal origin and its environment. Here we discuss each of these points in turn.

Brood signatures

We found that tree swallow broods can be discriminated from one another by their calls, with six of the nine call features we measured differing significantly amongst control broods (Table 3). These results are consistent with a previous study on tree swallows, which examined fewer call features than the present study, but also showed that siblings are acoustically more similar than non-siblings in the duration and frequency structure of their calls (Leonard et al. 1997a). The results are also consistent with a study on cliff swallows, which showed that 82% of nestlings could be assigned to the correct brood based on their call features (Medvin et al. 1992).

Of course, the existence of similarity in call features between siblings only indicates the potential function of these features as a brood signature for parent-offspring recognition. Playback experiments, ideally conducted directly after fledging, are needed to confirm the use of brood

Table 3. Variance components for begging calls of tree swallow nestlings in control and cross-fostered nests. Bold typing indicates statistically significant contributions to the variance in each call measure (** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$).

		Variance components						
		Control nests			Cross-fostered nests			
		Nestling	Nest	Residual	Nestling	Rearing	Origin	Residual
Duration (ms)		0.26***	0.51**	0.23	0.23***	0.43**	0.00	0.38
Amplitude modulation (ms^{-1})	variance	0.06	0.23**	0.71	0.20***	0.04	0.00	0.76
Frequency (Hz)	mean	0.36***	0.47**	0.17	0.68***	0.04	0.00	0.28
Frequency modulation ($^\circ$)	mean	0.49***	0.24	0.26	0.57***	0.09	0.10	0.24
Frequency modulation ($^\circ$)	variance	0.14**	0.28*	0.58	0.50***	0.04	0.01	0.45
Entropy	mean	0.29***	0.47**	0.24	0.48***	0.00	0.00	0.52
Entropy	variance	0.37***	0.18	0.45	0.31***	0.22*	0.00	0.47
Pitch (Hz)	mean	0.28***	0.48**	0.24	0.71***	0.00	0.00	0.29
Pitch goodness	mean	0.52***	0.00	0.48	0.45***	0.25	0.00	0.30

signatures by parents, as shown in colonial species of swallow (Beecher 1991). Experiments to date have shown no such recognition in the semi-colonial tree swallow, but they were all conducted before fledging, when parents might still be using the simple rule of feeding any young in their nest (Leonard et al. 1997a, Whittingham et al. 2003).

Genetic/maternal effects

Brood of origin had relatively little influence on the call features we measured. In contrast, an earlier study on the closely related cliff swallow found that unrelated, cross-fostered nestlings did not share call features, and therefore assumed that sibling-sibling similarity must be largely genetically determined (Medvin et al. 1992). In the latter study, cross-fostering took place at the egg stage and the eggs were not marked, so the authors could not identify true siblings to compare their calls and obtain a direct estimate of genetic influence on call similarity (Medvin et al. 1992). Two cross-fostering experiments on barn swallows *Hirundo rustica* showed that relatedness among nestlings affects the call duration and amplitude (Boncoraglio and Saino 2008, Boncoraglio et al. 2009). However, in both cases, cross-fostered nestlings were contrasted with host nestlings remaining in the nest, so environmental and genetic/maternal effects could not be distinguished.

Strictly genetic determination of brood signatures might not be adaptive for nestlings because of the high likelihood that they are unrelated to the parents that are caring for them. In tree swallows, in particular, at least half of nestlings are sired by males other than the male attending the nest (Barber et al. 2005). Thus nestlings might benefit by not revealing their genetic origins, so that they can extract as much care as possible from attending adults, who might not be their own genetic parents (Whittingham and Dunn 2001, Whittingham et al. 2003). Because our experiment only addressed maternal, and not paternal, inheritance, however, this argument assumes that selection against revealing paternity would necessarily select against revealing maternity, which may not be the case.

Rearing environment

The begging calls of nestlings in cross-fostered nests tended to be more similar than the calls of true siblings growing up in different nests, suggesting that the rearing environment had a stronger effect on call structure than genetic/maternal effects. There are several mechanisms by which offspring in the same nest might produce similar calls. Most obviously, nestlings growing up in the same nest may experience similar feeding rates and therefore be in similar condition (Leonard et al. 2000), leading to similarities among all call features that correlate with condition (Leonard and Horn 2006).

Alternatively, because nestlings are known to adjust their calls in response to noise levels at the nest (Leonard and Horn 2005) and other acoustic characteristics of the nest (at least in natural cavities; Fairhurst et al. 2013), nestlings in a shared acoustic environment will likely develop similar calls. Nestlings might also model their calls on the calls of their foster parents, as has been shown in other

species (Berg et al. 2012), in which parents give provisioning calls in similar context to tree swallow parents (Leonard et al. 1997b). Finally, calls within a nest might be more similar because of call convergence among brood mates. Leonard and Horn (2001b) have previously demonstrated that nestling tree swallows adjust their begging calls when begging with another sibling to become more similar in overall structure, specifically call duration (see also Roulin et al. 2009). Indeed, in the current study nest of rearing had its greatest influence on call duration, with 43% of the variation in call duration attributable to the rearing environment. Further experiments could test these alternative explanations for the rearing effects seen in the present study.

Gene/maternal \times environment interactions

Our results show that begging calls of nestlings are neither affected by their genetic/maternal origin nor by their rearing environment alone. This suggests that, in natural conditions, brood signatures develop through an interaction between the rearing environment and genetic/maternal effects. One possible mechanism for such an effect may be that a nestling's genetic/maternal background makes the nestling physically more likely to match the call structure of a brood full of true siblings than to match unrelated nestlings. Alternatively, very early exposure (i.e. before cross-fostering at three days) to parental calls might prime nestlings to respond to those parental calls in a particular way later on, especially given recent discoveries that nestling birds attend to parental calls even before hatching (Colombelli-Négrel et al. 2012).

Evolution of brood signature development

The dependence of call development on an interaction between genetic/maternal and environmental factors raises the intriguing possibility that call development in tree swallows is the outcome of parent-offspring conflict over whether nestlings should expose or conceal their genetic identity. Nestlings, for their part, might attract more care from parents by aligning their calls with those of their brood mates or modelling their calls on the vocalizations of their parents. Parents, on the other hand, might best direct care to their own genetic offspring by constraining the plasticity of call development in their nestlings. Of course, while such conflict is expected theoretically (Lacy and Sherman 1983) and has been shown in other kin recognition systems (Adams 1991, van Zweden et al. 2009), this suggestion is purely speculative. More information is needed on the exact means by which parents affect nestling call development, and especially what means work especially effectively on their own genetic offspring – both interesting issues in vocal development, whether or not they are the result of parent-offspring conflict.

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