

## Parent–offspring recognition in tree swallows, *Tachycineta bicolor*

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**Abstract.** Parent–offspring recognition appears to be highly developed in species in which the risk of misdirecting care is high (e.g. colonial species). Some of the best evidence for this relationship comes from comparative work on swallows of the family Hirundinidae. Using methods followed in earlier studies, we determined whether parent–offspring recognition occurs in the tree swallow, *Tachycineta bicolor*, a non-colonial species closely related to the highly colonial bank swallow, *Riparia riparia*, and the solitary rough-winged swallow, *Stelgidopteryx ruficollis*. Parents did not discriminate between playbacks of the calls of their own versus non-related nestlings. However, older nestlings called more in response to playback of parental calls than non-parental calls, suggesting that they recognized their own parents. Despite significant individual variation in parental and nestling calls, variation in tree swallow nestling calls was lower than analogous calls in the bank swallow. Our results provide further support for a positive relationship between recognition, individual variation in call structure and coloniality.

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Natural selection should favour parents that preferentially direct care to their own offspring. In most species, the risk of providing care to unrelated young is relatively low. In colonial species, however, where young from several litters or broods mix at various stages, the probability of misdirecting care is increased. In these species, parents could benefit from the ability to recognize their own offspring (e.g. Buckley & Buckley 1972; Beer 1979; Stoddard & Beecher 1983; Lessells et al. 1991).

The offspring of colonial species may also benefit from recognizing their parents. For instance, young that indiscriminately solicit care risk attack and injury from adults that are capable of recognizing offspring (e.g. Evans 1980; Beecher 1982; Proffitt & McLean 1991). Also, recognition of parents by offspring decreases the likelihood of mistakes by the parent (Beecher 1981). Thus, parent–offspring recognition should be adaptive for both parents and young in situations where there is a risk of misdirecting care.

For parent–offspring recognition to occur, cues must be available to allow parents and young

to identify each other. Such cues include signature traits such as individually distinctive calls (Loesche et al. 1991) or odours (Holmes 1990). In species where parent–offspring recognition is well developed, these cues often appear immediately before the young intermingle with non-kin (e.g. Beecher et al. 1981).

Some of the best evidence for parent–offspring recognition comes from comparative work on swallows (family Hirundinidae; e.g. Beecher et al. 1981, 1985; Stoddard & Beecher 1983; Sieber 1985; Medvin & Beecher 1986). In colonial species such as bank swallows, *Riparia riparia*, and cliff swallows, *Hirundo pyrrhonota*, parents respond preferentially to the playback of begging calls of their own versus alien (i.e. unrelated) nestlings (Beecher et al. 1981; Stoddard & Beecher 1983). The young of these species also recognize their parents' calls (Beecher et al. 1985; Sieber 1985). In the non-colonial barn swallow, *H. rustica*, and the solitary rough-winged swallow, *Stelgidopteryx ruficollis*, however, recognition is poorly developed (Beecher 1981; Medvin & Beecher 1986). Not surprisingly, the calls of cliff and bank swallows are more individually distinctive than the calls of barn and rough-winged swallows (Beecher 1991; Medvin et al. 1993; Beecher et al.

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1985). Taken together, these results suggest that parent-offspring recognition and cues for recognition are adaptations for colonial nesting in swallows.

The purpose of our study was to examine parent-offspring recognition and vocal cues for recognition in tree swallows, *Tachycineta bicolor*. This species is ideal for such a study for several reasons. First, recent phylogenies based on DNA-hybridization (Winkler & Sheldon 1993) show that tree swallows are closely related to the well-studied bank and rough-winged swallows, making comparisons particularly interesting. Furthermore, tree swallows appear to have nesting habits that are intermediate to those of the highly colonial bank swallow and the solitary rough-winged swallow. That is, tree swallow pairs defend an area around the nest and will nest semi-colonally (Wheelwright et al. 1991) or solitarily (Muldal et al. 1985) depending on the distribution of nest sites. Fledgling tree swallows from up to four families may be found together in the week following fledging, and newly-fledged young often visit the nestboxes of other tree swallows in the area (M. Leonard & A. Horn, unpublished data). Thus, unrelated young may mix during the dependent period, although not to the extent found in highly colonial species. Tree swallows may therefore be expected to show levels of recognition and variation in call structure intermediate to those of bank and rough-winged swallows.

An earlier study on parent-offspring recognition in tree swallows (Burt 1977) showed that broods that were moved into 'foreign' nests at day 17 fledged earlier than control broods which were removed and then returned to their own nest (i.e. were sham-moved). Experimental nestlings may have fledged earlier because they recognized a difference in the nest and/or the adults. Alternatively, the adults may have recognized that the exchanged nestlings were not their own and treated them differently (Burt 1977). Whatever the case, these results suggest the possibility that some form of recognition exists in tree swallows.

In this study, we used methodologies followed by Beecher and co-workers, so that our results could be more directly compared to their earlier studies of parent-offspring recognition in other species of swallows. These methods consist of (1) the playback of nestling begging calls to parents in a two-speaker design; (2) the playback of parental and non-parental calls to nestlings in a single

speaker design, (3) ANOVA on individual variation in parental and nestling calls, and (4) sibling-sibling analysis of nestling calls (as done for cliff and barn swallows; Medvin et al. 1992).

We emphasize that we use the term 'recognition' in a broad sense. Failure to discriminate between two stimuli, for example during a playback experiment, may indicate either a perceptual inability to discriminate or a failure to respond differently, even though the difference was perceived (e.g. Beecher 1991). In this study, we tested whether tree swallows show discrimination in situations in which other species of swallows have been tested. We did not test whether tree swallows are perceptually capable of parent-offspring discrimination.

## METHODS

We conducted the study in King's County, Nova Scotia, Canada between 1 May and 30 June 1995. The study site was an open field by a river with 26 tree swallow boxes placed at 10-m intervals around its periphery. Each nestbox measured approximately 30 × 15 × 15 cm (internal dimensions) with the hole centre about 20 cm above the floor. This site had a mean occupancy rate of 73% between 1994 and 1996. In 1995, 77% of the boxes at this site were occupied.

We trapped adults using nestbox traps (Stutchbury & Roberston 1986) and individually marked them with acrylic paint and coloured leg bands. First-egg dates and hatching dates were determined by checking nestboxes every second day until 2 days before the predicted hatching date, after which they were checked daily.

### Parental Recognition of Offspring

We played nestling begging-calls to tree swallow parents to determine whether they discriminated between the calls of their own nestlings and those of nestlings from another brood. Nestling begging-calls were recorded at 16 nests when the nestlings were aged 8–10 days (mean, 9.2 days; i.e. younger nestlings) and 15–18 days (mean, 15.7 days; i.e. older nestlings). The calls were recorded within 24 h of a playback using a Realistic lapel microphone taped to the inside of the nestbox. The microphone was attached to a Marantz PMD222 portable cassette recorder which was

operated by an observer located 18 m from the nestbox. Begging calls were recorded during parental feeding visits.

The taped calls were digitized at 8 bits and a 22-kHz sampling rate using SoundEdit (Farallon, Berkeley) software. Using the same software, we high-pass-filtered the calls at 2 kHz to reduce background noise. We then recorded the calls onto Sony metal SR cassette-tapes in a program consisting of 5 s of begging calls (delivered at natural rates as they were recorded) followed by 5 s of silence, repeated 30 times for 5 min. Each 5-s sequence contained the calls of at least three nestlings. Within each trial, the experimental tape included the begging calls of the test parents' own nestlings, and the control tape included begging calls of nestlings from another nest matched for age and brood size. We did not use recordings from nests neighbouring the experimental nest, and each recording was used only once as an 'own' and once as an 'alien' treatment.

Approximately 24 h before a playback, we placed two empty nestboxes (i.e. test boxes) 1.5 m on either side of the box selected for playback (i.e. home box). The test boxes were identical to the home box, and their openings were oriented in the same direction as that of the home box. On the following day, we placed a Realistic 40-1259B Speaker Amplifier in each of the test boxes and connected them by an 18-m cable to a Sony WM-AF54 cassette-player. Approximately 30 min after setting up the speakers, we removed the nestlings from the home box and blocked its opening with a piece of cardboard. Own and alien begging calls were then played simultaneously, one from each speaker, by an observer blind to which tape was playing from which speaker. The volume of the playbacks was adjusted to natural levels and kept constant and equal throughout the study. Across trials we alternated own and alien calls between the left and right speaker.

During the playback, we recorded the following information (Beecher et al. 1981; Medvin & Beecher 1986) onto a cassette tape recorder for later transcription: (1) which test box was first approached within 1 m; (2) how many passes were made within 1 m of a test box; (3) how many contacts were made with the test box. The last category included the number of times an adult landed on the test box, perched at the opening or hovered in front of the opening. We did not

distinguish between the responses of male and female parents.

In species with well-developed recognition, the ability to discriminate develops a few days before the young leave the nest (e.g. Beecher et al. 1981; Lessells et al. 1991), in some cases correlating with the development of stereotyped, individually distinctive calls (e.g. Beecher et al. 1981). In our population, the average age at fledging is 18 days (range, 15–22), and nestling calls appear to be stereotyped by day 15 (A. Horn, unpublished data). We conducted playbacks both when nestlings were approximately 9–11 days old ('younger' nestlings) and again when they were 16–19 days old ('older' nestlings). Playbacks to older nestlings should thus have been late enough to detect recognition if it were occurring.

### Offspring Recognition of Parents

In a second experiment, we played parental contact calls to nestling tree swallows to determine whether they discriminated between the calls of their own parents and those of other adults. Parental calls were recorded at 16 nests when nestlings were 3–5 days old. A Realistic lapel microphone was placed inside each nestbox, and the calls given by parents on regular visits to the nest (M. Leonard, unpublished data) were recorded using a Marantz PMD 222 portable cassette-recorder. No distinctions were made between the calls of male and female parents.

Contact calls were digitized and high-pass-filtered as described earlier. We created a 5-s sequence composed of two parental contact calls (each approximately 0.15 s long) given 1 s apart, followed by approximately 3.85 s of silence. This sequence was repeated 12 times to produce a 1-min tape loop. Experimental tape loops consisted of the calls of the test nestlings' own parents (i.e. parental calls), and control tape loops included the calls of parents from another nest (i.e. non-parental calls). Both experimental and control tapes were free of nestling begging calls.

Playbacks were presented to 16 groups of nestlings when they were 8–11 days old (mean, 10.1 days; i.e. younger) and again when they were 14–17 days old (mean, 15.3 days; i.e. older). Nests were paired to allow each loop of contact calls to serve once as a parental test call and once as a non-parental test call, so that differences in the calls were counterbalanced.

Before each trial, three randomly chosen nestlings were removed from their home box and placed in a test box that was identical to the home boxes and lined with tree swallow nesting material. The test box was a minimum of 20 m from each home box. A Plexiglas plate was placed in the opening on the hinged side of the test box and a wooden frame covered by a dark plastic bag was placed around that side of the box. A Panasonic PV-900-K VHS video-camera mounted on a tripod was then placed under the covered frame, and the response of the nestlings to playback calls was videotaped. We tested nestlings away from their home box so that the alarm calls of adult tree swallows would not interfere with the trials. We waited at least 2 min after nestlings were moved into the test box or until they were resting quietly with their heads down before beginning the playback.

The contact calls were played through a Realistic 40-1259B speaker amplifier, held 20 cm from the opening of the nestbox and connected to a Marantz PMD-222 portable cassette recorder. The speaker was held adjacent to the entrance, rather than over it, to prevent shadows from falling across the opening. The volume was adjusted to natural levels and kept constant throughout the trials. Experimental and control presentations were separated by at least 2 min of silence to allow the nestlings to return to a resting position. The order in which parental and non-parental calls were presented was alternated between trials. Nestlings were returned to their home box after the completion of the trials. The same procedure was used for younger and older nestlings, except that older nestlings were given at least 10 min to acclimatize to the test box.

Nestling responses to parental and non-parental calls were recorded as the proportion of intervals following the playback of a call (maximum=12) in which at least one nestling (a) raised its head without gaping, (b) gaped or (c) called.

### **Acoustic Analyses of Calls**

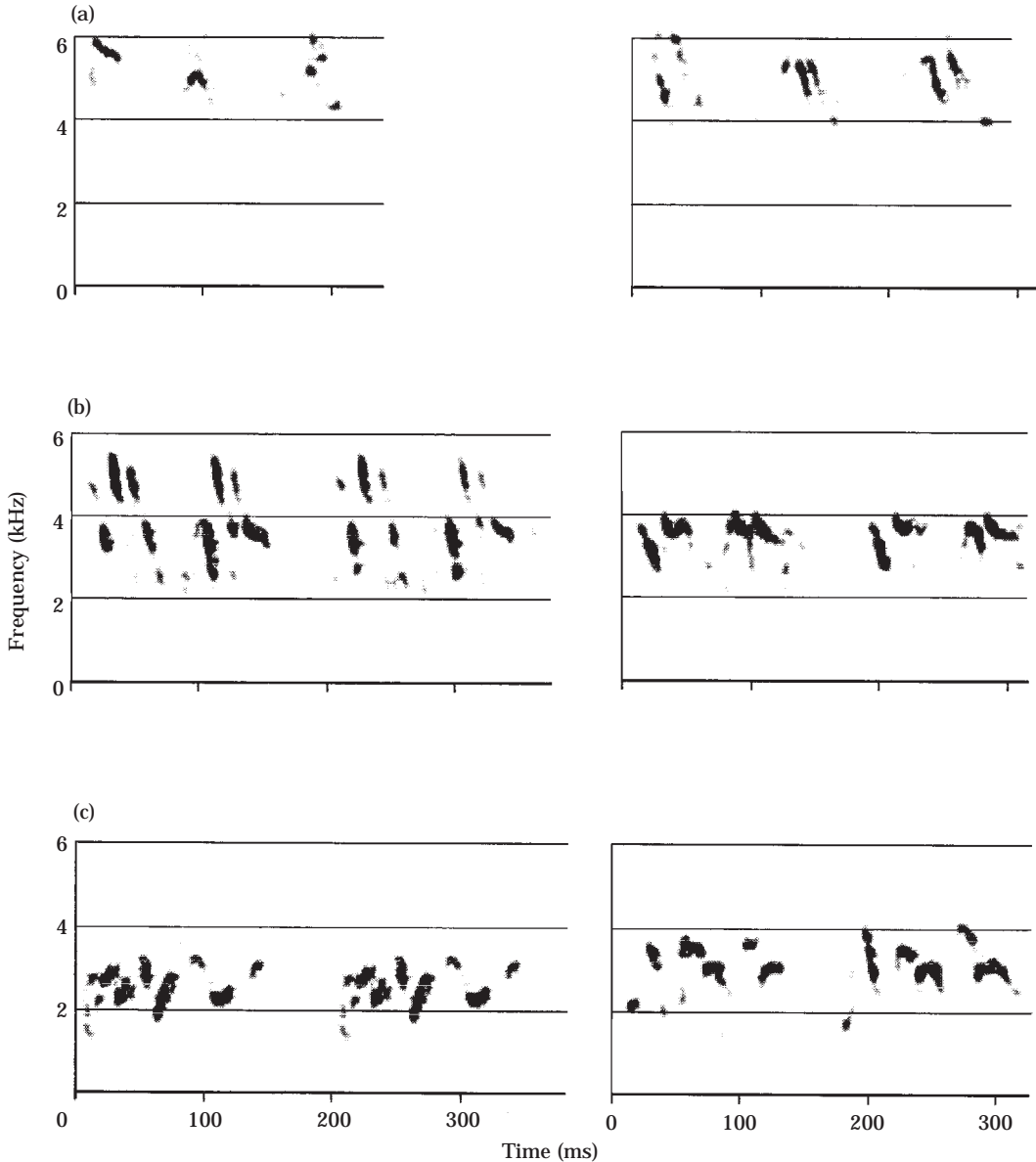
We examined individual variation in the calls of both nestlings and adults to determine whether acoustic cues for recognition existed in this species. We also examined the similarity in the calls of siblings to determine the possibility of brood signatures. The calls used to examine

individual variation in nestling vocalizations were taken from the response videos of nestlings made during the study of offspring recognition of parents (above) and from videotapes of broods made during a separate study in 1994 (Leonard & Horn 1996). In this way, we could see which nestling called and could obtain recordings from known individuals. Calls used to examine the similarity of these vocalizations between siblings were taken from the recordings of older nestlings made during the study of parental recognition of offspring. We were unable to obtain calls of enough sibling pairs to do this analysis for younger nestlings. Adults calls were taken from the videotapes made in 1994.

We analysed individual variation in call structure by measuring four calls from each of 10 younger nestlings (10 days old), 10 older nestlings (15 days old) and 10 each of adult males and females. We analysed similarity between siblings using one call from each nestling in 16 pairs of siblings from different nests. In all cases, the selected individuals and calls were the first encountered that had a signal that could be measured consistently. For all calls we measured time characters using SoundEdit, and measured frequency characters by playing calls at one-eighth speed through a Unigon Model 4500 spectrum analyser at an analysis range of 2 kHz, yielding an effective bandwidth of 160 Hz.

The calls of younger nestlings are quite variable. They generally consist of one to three short (less than 50 ms) pure-tone elements (i.e. continuous traces on the sonagram) that usually drop sharply in frequency (Fig. 1). The calls of older nestlings are more invariant from one repetition to the next. They consist of two calls, each approximately 80 ms long, with about 20 ms between the calls (Fig. 1). Each call consists of three to five figures or phrases (i.e. elements arranged in a consistent pattern) that usually decrease sharply in frequency while being rapidly amplitude-modulated. The second call is usually a clearer repetition of the first, so we measured the second call only. Parental calls are approximately 150 ms long, and contain alternating high and low elements which usually form a repeated figure or phrase (Fig. 1).

To test for inter-individual variability in call structure, we examined features of the calls that could be measured consistently and that were analogous to features analysed in studies of other



**Figure 1.** Sonograms of representative nestling begging-calls and parental contact-calls of tree swallows: (a) two 10-day-old nestlings (three calls each); (b) two 15-day-old nestlings (two calls each); (c) two adults (one male and one female, two calls each).

swallows (Beecher et al. 1981, 1985; Sieber 1985). Three measures described the overall structure of the calls and were taken on all nestlings and adults: call duration (ms), frequency of the first figure, measured at its first inflection point (Hz) and frequency range of call, measured from the

highest to the lowest discernible frequency peak in the entire call (Hz). In addition, unlike the calls of younger nestlings and parents consisted of repeated figures. In these cases we also measured figure duration, which is the time (ms) between the start of successive

figures, averaged across the call. Finally, to describe the change in frequency that often occurred over the course of the calls of older nestlings only, for older nestlings we measured the average difference in frequency between the inflection points of successive figures (Hz).

We analysed inter-individual variation in call structure with ANOVAs on each variable. This method compares the amount of inter-individual variation relative to intra-individual variation. In addition to measuring individual variation in calls, we also wanted to determine whether different broods varied significantly in call structure. If so, then parents could possibly discriminate between their own and alien nestlings by attending to features of the call that varied significantly among broods, rather than by having to recognize each of their young individually. To test whether siblings tend to have similar calls compared to unrelated individuals, we did a repeated-measures ANOVA, using broods as blocks, and reporting the ratio of the between-brood variance to the total variance ( $r'$ , the intra-class correlation). This is the sibling-sibling analysis well known in genetics, but only recently applied to animal signals (nestling barn and cliff swallows; Medvin et al. 1992).

## RESULTS

### Parental Recognition of Offspring

Adult tree swallows responded in 11 of 16 trials involving playbacks of the begging calls of younger nestlings and 14 of 15 trials involving playbacks of the calls of older nestlings.

Parent tree swallows did not appear to discriminate between their own and alien nestling calls at either younger or older nestling stages. The number of first approaches, passes or contacts by parents to test boxes with playbacks of their own nestlings and test boxes with playbacks of alien nestlings did not differ significantly (Table I). A power test (Taylor 1990) showed that we had at least a 90% chance of detecting a difference of at least 1.6 units for younger nestlings and 3.1 units for older nestlings, had such differences existed.

### Offspring Recognition of Parents

Younger nestlings responded to playbacks of adult calls in 15 of 16 trials; older nestlings

**Table I.** Number of first approaches, mean  $\pm$  SE number of passes and contacts (hovers by or lands on) with test boxes playing recordings of the begging calls of the test parents own offspring and those of alien (i.e. unrelated) young

Response	Own calls	Alien calls	<i>P</i>
Younger			
Approaches	7/11	4/11	0.27
Passes	1.7 $\pm$ 0.50	0.9 $\pm$ 0.30	0.15
Contacts	2.2 $\pm$ 0.60	3.6 $\pm$ 1.60	0.46
Older			
Approaches	4/14	10/14	0.09
Passes	2.8 $\pm$ 0.60	3.6 $\pm$ 1.00	0.38
Contacts	3.6 $\pm$ 1.10	3.8 $\pm$ 1.30	0.83

Begging calls were recorded when nestlings were aged 8–10 days (younger) and 15–18 days (older). Number of first approaches was compared using a binomial test; passes and contacts were compared using Wilcoxon's signed-ranks test.

**Table II.** Mean  $\pm$  SE proportion of playback intervals in which younger (i.e. 8–11 days old;  $N=15$ ) and older nestlings (14–17 days old;  $N=12$ ) raised their heads without gaping, gaped or called in response to parental and non-parental contact calls

Response	Parental	Non-parental	<i>z</i>	<i>P</i>
Younger				
Head raised	0.4 $\pm$ 0.10	0.5 $\pm$ 0.10	-1.0	0.30
Gapes	0.1 $\pm$ 0.10	0.2 $\pm$ 0.10	-1.1	0.29
Calls	0.4 $\pm$ 0.10	0.5 $\pm$ 0.10	-1.1	0.29
Older				
Head raised	0.6 $\pm$ 0.10	0.7 $\pm$ 0.10	-1.0	0.32
Gapes	0.1 $\pm$ 0.003	0.1 $\pm$ 0.004	-1.5	0.14
Calls	0.5 $\pm$ 0.10	0.3 $\pm$ 0.10	-2.4	0.01*

Responses were compared using Wilcoxon's signed-rank test.

responded in 12 of 13 trials. Younger nestlings did not appear to discriminate between parental and non-parental calls (Table II). Older nestlings, however, called significantly more often in response to parental calls than to non-parental calls (Table II).

### Acoustic Analyses of Calls

The calls of both younger and older nestlings differed significantly among individuals for all variables measured (Table III). Moreover, for older nestlings, siblings tended to be more similar

**Table III.** *F*-ratios and associated *P*-values from ANOVAs on inter-individual variation in acoustic features of calls of younger (10-day-old) and older (15-day-old) tree swallow nestlings, using four calls per nestling

Variable	Younger nestlings		Older nestlings	
	$F_{9,30}$	<i>P</i>	$F_{9,30}$	<i>P</i>
Call duration	4.27	0.0012	8.69	0.0001
Figure frequency	4.16	0.0015	7.94	0.0001
Frequency range	3.49	0.0046	5.45	0.0002
Figure duration	—	—	11.25	0.0001
Frequency difference	—	—	3.81	0.0026

**Table IV.** *F*-ratios and associated *P*-values from ANOVAs on inter-individual variation in acoustic features of calls of 10 male and 10 female parents, using four calls from each individual

Variable	Females		Males	
	$F_{9,30}$	<i>P</i>	$F_{9,30}$	<i>P</i>
Call duration	2.10	0.06	5.00	0.0004
Figure duration	1.55	0.18	2.97	0.01
Mean frequency	6.64	0.0001	17.86	0.0001
Frequency range	10.96	0.0001	30.00	0.0001

to one another in call duration and frequency than were nestlings from different nests (results of sibling-sibling analysis: duration  $r'_{14,15}=0.16$ ,  $P=0.008$ ; figure frequency:  $r'_{14,15}=0.10$ ,  $P=0.04$ ). The other variables did not show significant similarity between sibling pairs (all  $r'_{14,15}\leq 0.04$ , all  $P\geq 0.17$ ).

Female parents had calls with significantly higher mean frequencies than those of male parents (females:  $3930 \pm 55$  Hz, males:  $3730 \pm 81$  Hz, nested ANOVA  $F_{1,18}=4.83$ ,  $P=0.04$ ). The other features of the calls did not differ between the sexes (all  $F<1.29$ , all  $P>0.27$ ), but we nevertheless tested each sex separately for individual variation. Both sexes showed significant individual variation in mean frequency and frequency range (Table IV); male calls also varied significantly in call and figure duration (Table IV).

## DISCUSSION

Parent tree swallows did not preferentially respond to their own young, despite significant

variation in the calls of individual nestlings and broods. The forced choice test used in all field playbacks to parent swallows, including ours, is probably the most sensitive paradigm for testing discrimination (Beecher 1991). As in any field experiment, failure to discriminate does not imply that parents are incapable of perceiving individual variation in calls, nor that parents would not discriminate in other situations (e.g. Loesche et al. 1991). Thus, the field results for swallows apply specifically to the situation in which a parent is forced into a choice of searching for its nestlings at two locations. In our experiment, adults responded to the playbacks with searching behaviour (e.g. passing by boxes or hovering in front of nest openings) in 73% of trials at younger nestling stages and in 93% of trials at older stages, suggesting that the playback set-up was an adequate simulation of the searching problem.

The results of our playbacks to tree swallows were intermediate to previous results for their closest relatives, rough-winged and bank swallows. Similar playback experiments on a small sample of rough-winged swallows, which are solitary nesters, showed no recognition by parents of offspring or vice versa (M. Beecher & I. Beecher, unpublished data, cited in Beecher et al. 1986), but experiments on bank swallows, which are highly colonial, showed reciprocal recognition (Beecher et al. 1981; Sieber 1985). Tree swallows, which are semi-colonial in most populations, showed offspring recognition of parents but not the reverse (this study). This pattern of recognition supports the proposed relationship between degree of coloniality and degree of recognition (Beecher 1991).

The results of our study are most consistent with those reported from an earlier study on barn

swallows (Medvin & Beecher 1986). That is, parent barn swallows also did not appear to discriminate between their own and unrelated young (Medvin & Beecher 1986). Unlike the highly colonial cliff and bank swallows, barn swallow chicks do not move between nests, and family groups mix relatively infrequently after fledging (Medvin & Beecher 1986). Although tree swallow fledglings do intermingle in small groups and occasionally enter the nests of other birds, the degree of mixing is much less than in colonial species, where nests are often in high densities and young crèche after fledging. Thus, the costs to parent tree swallows of mistakenly rejecting their own young may outweigh the benefits of discrimination.

A potential selective force for recognition by parent tree swallows, especially males, is the high degree of extra-pair fertilizations (50–87% of broods) documented in some populations (Lifjeld et al. 1993; Dunn et al. 1994). Although we have not examined this factor in our population, if males had a high probability of having extra-pair young in their nest, then discrimination should be favoured. Alternatively, females and extra-pair young would benefit from the males' inability to recognize their own nestlings and thus there may be counterselection on nestlings to suppress cues for recognition. The similarity in calls between siblings in our population is relatively low (see below), suggesting that nestlings are not imitating the calls of siblings or parents, as expected if they were attempting to suppress cues. Again, it is not clear how the benefits of recognition by male parents would balance against the potential costs of discriminating between potentially subtle differences in cues.

Parents may use cues other than individual recognition when offspring from only a few broods intermingle. For instance, parents could use locational cues to find their young if individual offspring remain in one area for an extended period of time. Alternatively, the ability of older offspring to recognize their parents, as observed in this study, may be sufficient to prevent parents from provisioning unrelated young (e.g. Beer 1979; Medvin & Beecher 1986). Indeed, fledgling tree swallows will often approach their parents as they return to the young with food (M. Leonard & A. Horn, unpublished data).

As in tree swallows, barn swallow offspring called more in response to the playback of

parental calls than they did to non-parental calls, suggesting that they recognized their parents (Medvin & Beecher 1986). It is not clear what selection pressures favour recognition of parents by young, since chicks should benefit from soliciting parental care from all adults (e.g. Falls 1982). Several factors may, however, select against indiscriminate treatment of adults by young tree swallows. For instance, during fledging, parents call to their nestlings, apparently to encourage fledging and to keep the family group together (M. Leonard & A. Horn, unpublished data). The ability of the young to recognize these calls may be important for keeping them within the relative safety of the family unit during this time. In addition, after fledging, young tree swallows often fly from perches to intercept their parents returning with food (M. Leonard & A. Horn, unpublished data). Indiscriminate responses to all passing adults could waste energy, provoke attacks by non-breeding adults and also increase the risk of predation (Medvin & Beecher 1986).

Species of swallows that show strong parent-offspring discrimination also have nestling calls with more inter-individual variation (Beecher 1982; Medvin et al. 1993). The  $F$ -values in Table III are a measure of this variation and can be compared to other studies by transforming them to information capacity,  $H_s$ , measured in bits.  $H_s$  for any given variable is a transformation of the ratio of the total to the within-individual variation in the call and, unlike  $F$ , does not vary with sample size:

$$H_s = \log \sqrt{\frac{\sigma_B^2 + \sigma_W^2}{\sigma_W^2}} = \log \sqrt{\frac{F + n - 1}{n}}$$

The total  $H_s$  for the call is the sum of  $H_s$  for all the variables, if the variables are independent. If the variables are intercorrelated, the intercorrelations are first removed by principal components analysis and then the total  $H_s$  is the sum of the  $H_s$  for the factor scores on each new axis (in this case, the number of axes extracted equals the number of original variables; Beecher 1989). In either situation, the higher the value of  $H_s$ , the more the calls vary and therefore the more potential they have for encoding individual identity (Beecher 1989).

Our analysis of the calls of nestling tree swallows indicated an information capacity of



3.34 bits, or 3.20 bits when variable inter-correlations (here,  $|r_9| \leq 0.59$ ,  $P \geq 0.07$ ) are removed using principal components analysis. These values are similar to the information capacity of other non-colonial swallows (rough-winged swallows: 3.2 bits; barn swallows: 4.57 bits), which in turn are lower than those of the colonial species (bank swallows: 10.2 bits; cliff swallows: 8.74 bits; Beecher 1991). Thus our results lend further support for a positive relationship between coloniality and individual variation in call structure (Medvin et al. 1993).

We also found lower sibling-sibling similarity in tree swallow nestlings than in the other swallows that have been analysed. The test statistic for sibling similarity, the intra-class correlation or  $r'$ , can vary from 0 (no sibling similarity) to 1 (siblings identical). Intra-class correlations for tree swallows appear to be low compared to the other species that have been tested (tree swallows:  $r' \leq 0.16$ ; barn swallows:  $r' \geq 0.18$ ; cliff swallows:  $r' \geq 0.27$ ; Medvin et al. 1992). Since cliff swallows are strictly colonial, and barn swallows are non-colonial, this pattern supports the hypothesis that sibling-sibling similarity is an adaptation to colonial living (Medvin et al. 1992), although a comparison with a species more closely related to tree swallows would be more convincing.

For parental calls, comparative information on call differentiation is not available, although both tree and bank swallows (Sieber 1985), show significant individual variation in male and female calls. Parental calls are important in parent-offspring interactions before and after fledging, so one might expect individual variation to be particularly strong in colonial species (Sieber 1985). However, parental calls are also used in interactions between parents (Robertson et al. 1992; M. Leonard, N. Fernandez & G. Brown, unpublished data), which might select for individual distinctiveness, even in non-colonial species like tree swallows.

Interspecific comparisons of both call structure and responses to playback depend on a number of assumptions (Beecher 1989). Perhaps the most important of these are that the variables measured describe exhaustively the features relevant to the birds themselves, and that the variables scale in the same way that the birds would scale them. Our measures of call features are probably not exhaustive. For example, they do not describe the

variation in the form of nestling and parental calls apparent in Fig. 1 (see also Beecher et al. 1981). Even if they were, the birds may weigh frequency, for example, more heavily than temporal features (e.g. Weary 1990), making analyses that weighed the two features equally less important biologically (Beecher 1989). Similarly, our playbacks are context-dependent, so both parents and offspring could show stronger recognition in other situations (Loesche et al. 1991). Given the similarity between our methods and those of previous studies, our results lend support to a positive correlation between coloniality, call differentiation and parent-offspring recognition in swallows.

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