Investigating the role of call similarity in a tree swallow (*Tachycineta bicolor*) parent-offspring recognitionmechanism

"Are you my mother?"
- P.D. Eastman

Honours Thesis Research Project by

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Abstract

Parent-offspring recognition is a mechanism that allows parents and offspring to recognize each other by specific cues. The mechanism is predicted to be well developed in species that are at a high risk for misdirecting care awayfrom related individuals (e.g. colonial species). Tree swallows, a semi-colonial species, exhibit characteristics of parent-offspring recognition in the vocal interactions between older nestlings and parents. The design and ontogeny of the mechanism in tree swallows, however, is poorly understood. Call similarity between parents and nestlings from the same nest is one such design that facilitates recognition. We tested for similarity between the begging calls and contact calls of nestlings and parents from the same nest, and we used a cross-fostering experiment to determine if the similarity was derived from a learning mechanism or by genetic inheritance. We found very little significant evidence of similarity between nestling and parent calls from the same nest, either under the learning mechanism or the inheritance mechanism. Our results suggest that the parent-offspring recognition mechanism in tree swallows is not based on call similarities between nestlings and parents. However, the results may also suggest that call individuality is more important to the mechanism than call similarity. Further research is required to confirm the assumptions of our study.

1.0 Introduction

Recognition is an essential mechanism in the animal kingdom. Whether recognizing a different species, a mate or offspring, the ability to identify one's relationship with another individual can have a strong selective advantage,especially in social relationships. Kin recognition is the ability to distinguish a related individual from a non-related one. It allows individuals to locate their relatives in a complex matrix of unrelated conspecifics (i.e. individuals belonging to the same species) and exchange information and resources with true kin. This study focuses on parent-offspring recognition, a specific kin recognition mechanism that allows parents and their offspring to recognize each other.

The following study begins with an introduction to the study species, the research questions and the contributions of the study to environmental science. The introduction is followed by a review of relevant literature, in order to establish the theoretical framework of the study. The literature review leads into a description of the methods for data collection and data analysis that are employed to address the research questions. The study concludes with a presentation of the study results, a discussion of the results in the context of relevant literature, and, finally, the conclusions drawn from the discussion.

1.1 Study species *Tachycineta bicolor*

Tree Swallows (*Tachycineta bicolor*) are a passerine bird species. The species name *bicolor* comes from the distinctive dual colouring in mature adults: iridescent green-blue feathers on the body's upper-side and white feathers on the underside. They are medium-sized swallows, with adults typically 14 cm in length from bill tip to longest tail feather (Robertson, Stutchbury& Cohen 1992). Juveniles and 1-2 year old females

have grey-brown body feathers on the upper-side. Tree swallows primarily eat flying insects (Beal 1918) and tend to live in open areas, often near water where insects are numerous (e.g. fields, wooded swamps and shorelines) (Erskine 1977). Tree swallows are cavity nesters, relying on woodpeckers and rot to create tree holes for their nests (Robertson, Stutchbury& Cohen 1992). Because of their affinity for nesting in human-made nest boxes, adult and nestling tree swallows can be easily accessed for recordings during the nesting stage of their life history. This makes them ideal subjects for studying acoustic cues in parent-offspring recognition. Indeed, seminal research on parent-offspring recognition has used swallow species, including tree swallows, as study subjects (Halpin 1991).

Two important vocalizations in parent-offspring communication are the parent contact calls and the nestling begging calls. These calls are used while nestlings are in the nest, and are likely also used when nestlings leave the nest, a process known as 'fledging', which usually occurs when nestlings are 18-22 days old (Kuerzi 1941; Burtt 1977). Parents continue to feed the fledglings for at least 3 days after fledging (Kuerzi 1941), and because tree swallows sometimes nest in close proximity (10-15 m) to other tree swallow nests (Robertson and Rendell 1990), parents and fledglings must identify each other from other parents and fledglings flying in the vicinity. Tree swallows may use these contact and begging calls as recognition cues after fledging.

1.2 Research questions

The purpose of this study is to investigate theontogeny and design of a parent-offspring recognition mechanism in tree swallows. The first research question is whether the contact calls and begging calls of parent and their pre-fledging nestlings (18-22 days)

are similar, and thus could provide a mechanism for recognition. Older nestling tree swallows (14-17 days) respond more to their own parent's contact call than to a non-parent contact call, suggesting they recognize their parent's call (Leonard et al. 1997b). However, the mechanism through which they recognize the parent call is unclear. One hypothesis is that parents and nestlings recognize each other by acoustic similarities between the calls of parents and the calls of nestlings. There is evidence that thenestling begging calls ofcertain passerine species develop into adult calls, which implies common elements between the calls where similarities could occur. For example, the begging calls of chipping sparrows transition into templates for adult calls (Liu, Wada &Nottebohm 2009), and the contact call of great tits develops in the nest prior to fledging (Sharp 2003). This early call development is believed to help young generate vocal experience that can be applied later in life (Thorpe and Pilcher 1958), however it may also be relevant to a nestling's ability to recognize its own parent's call. Nestlings may develop their calls in the nest by listening to their parents' calls, and incorporating components of the adult call into their own calls. If the nestling learns its parent's call in this way, it may be that the nestling associates theacoustic parameters it learnswithits parent. Therefore when the nestling leaves the nest, it is able to recognize its parent by theacoustic parameters of the parent call it learned early in life. This is only possible under the assumption that adult calls are unique to each adult, and that the nestling is learning those same unique components. Only then can the nestling distinguish its parent from other adults.

The second research question asks if a learning mechanism or inherited phenotypesprimarily causesimilar features between the contact and begging calls.

Genetically determined cues may be unreliable due to recombination (Beecher 1988) and/or the high degree of extra-pair fertilizations (50–87% of broods) documented in some tree swallow populations (Lifjeld et al. 1993; Dunn et al. 1994). Alternatively, recognition cues developed by vocal learningare reliable if acquired at a time when there is good evidence of kinship (Sharp et al. 2005), such as when the nestlings are fed by parents in the nest. By learning and matching the calls of parents that provide for them, rather than inheriting a call phenotype that may be different from the providing parent (Mateo 2004), nestlings are more likely to sound like their provisioning parents, and thus, perhaps, be recognized by them. It is therefore likely that any similar components observed in the results will have a stronger learned component than a genetic component.

1.3 Applications to environmental science

The results of this project may reveal a subtle component of parent-offspring communication in tree swallows that has direct relevance to environmental science. Tree swallow habitat can sometimes be degraded by noise pollution, due to increasing chronic noise exposure from anthropogenic transportation and development in many terrestrial areas throughout North America (Barber et al. 2009). Leonard and Horn (2005) found that tree swallow nestlings would adjust their begging calls in the presence of ambient noise, which increased the likelihood that the call could be heard by their parents, but was also likely more costly to produce. One cost to this adjustment could be that it jeopardizes the parent-offspring recognition mechanism, in two specific ways. First, this acoustic adjustment to noise could also alter the acoustic component in the nestling call that the parent recognizes. Second, chronic noise exposure during the nesting stage could prevent nestlings from hearing and learning the unique parameters of their parents' calls.

Therefore, a better understanding of the parent-offspring recognition mechanism in tree swallows, which is the overall objective of this study, allows for better predictions of how it could be affected by noise pollution.

Tree swallows are a very successful and easily studied species in North America, and have been found ideally suited as a model for studying vocalbehavioural mechanisms (Leonard & Horn 1996, Leonard & Horn 2001a). As such, literature on tree swallow behaviour can be applied to research on other passerine species.This principle also has aconservation perspective, as the findings of this study may be extrapolated to endangered species closely related to tree swallows. The Bahama Swallow (*Tachycinetacyaneoviridis*) and the Golden Swallow (*Tachycinetaeuchrysea*), which belong to the same genus as *Tachycineta bicolor*, are both extremely rare species whose ranges have been severely reduced to only a few locations in the Bahamas and Jamaica, respectively, and both are experiencing declining population sizes (IUCN 2010). Because this makes studying these species difficult, it may be necessary to refer to literature on related species, such as tree swallows, to better understand these rare swallows. For example, literature specifically on swallow call similarity may help conservationists develop vocal identification protocols for monitoring the size and genetic variability in declining populations (Terry, Peake and McGregor 2005). Therefore, this study could directly contribute to conservation science.

Data collected during the course of this study may also contribute to climate change science. Increasing surface air temperatures during the breeding season over the last 60 years has advanced the first egg-laying date for tree swallows throughout North America, demonstrating that this species is directly influenced by climate change (Dunn

and Winkler 1999). Through the course of the project's field research, it was necessary to document the first egg-laying dates of 2010 for a tree swallow population in Wolfville, Nova Scotia. This data could contribute to further research on climate change, and be used to understand future effects of climate change on the species.

2.0 Literature review

The purpose of the literature review is to provide a context for the research questions stated in section 1.2:

1. Are there acoustic similarities between the nestling begging calls and parent contact calls in tree swallows?

2. If there are similarities, are they primarily influenced by a learning mechanism or genetic inheritance?

The review begins with an overview of literature relevant to parent-offspring recognition and communication in tree swallows, followed by an introduction to the concept of vocal learning and convergence, and concludes with a discussion of learning and inheritance with respect to parent-offspring recognition. The last two sections discuss issues with reproducing the study, and the delimitations imposed on the literature review.

2.1 Parent-offspring communication and recognition in tree swallows

Offspring have a selective advantage if they are able to solicit care from the individuals most invested in providing care. These individuals are typically their own parents, as parents have a selective advantage if they provide care to their own offspring (Leonard et al. 1997b). Selection for this advantage is greatest when the risk misdirecting care is highest. Species that raise their young in colonial environments, where the parents and offspring of several families are intermixed in a common space, are at a high risk of

confusing kin with non-kin, and there arebenefits to avoiding such mistakes. For example, offspring that beg specifically to their own parents reduce the risk of parents misdirecting care to non-offspring (Beecher, Stoddard &Loesche 1985). For offspring to solicit care from their own parents and for parents to provide care to their own offspring, both may require a recognition mechanism that allows them to locate kin within a matrix of non-kin. Birds will often use vocalizations as recognition cues (Jacot, Reers&Forstmeier 2010; Halpin 1991), as vocalizations are usually the primary means of communication within a species. These vocal cues are essential to parent-offspring recognition mechanisms that confer a selective advantage to the individuals that use them.

In tree swallows (*Tachycineta bicolor*), the primary calls between parents and offspring are the contact calls of parents and the begging calls of nestlings. The parent contact call is composed of 2-4 notes between 0.1-0.2 s in length, and the nestling begging call develops from a single weak, high-pitched note in the first week of life to 2-4 loud notes given in rapid succession by the third week (Robertson, Stutchbury& Cohen 1992). The contact call serves many functions for an adult tree swallow, including developing and maintaining adult pair bond, alerting the brooding female (Robertson, Stutchbury& Cohen 1992), and, in the context of parent-offspring communication, stimulating nestling begging (Leonard, Fernandez & Brown 1997a). The begging display of tree swallows nestlings is typical of many passerine species, which includes gaping with bright yellow gapes, posturing, and vocalizing loudly (Kilner&Johnstone 1997). The begging call of tree swallow nestlings is understood to encode information of offspring need to the parents, including warmth and hunger (Horn & Leonard 2002).

Because parents and offspring both use vocalizations to communicate with one another, parents and offspring both have the potential to present recognition cues to one another. This implies that parents may recognize their offspring's calls, and offspring may recognize their parent's calls. Both of these recognition patterns have been observed in colonial swallow species, such as bank swallows (*Ripariariparia*) and cliff swallows (*Hirundopirrhonota*) (Beecher, Beecher and Hahn 1981; Stoddard & Beecher 1983; Beecher, Stoddard and Loesche1985; Sieber 1985). Kin-recognition is likely an adaptation for colonial species (Leonard et al. 1997b), as recognition and individually distinctive calls are less well developed in non-colonial species, such as the barn swallow (*H. rustica*) and the solitary rough-winged swallow (*Stelgidopteryxruficolli*) (Beecher 1981; Medvin& Beecher 1986). Tree swallows are a semi-colonial species, nesting as solitary pairs or in larger aggregations (Robertson, Stutchbury& Cohen 1992). Therefore, they mayhave some degree of parent-offspring recognition. Indeed, Leonard et al. (1997b) demonstrated that nestling tree swallows are able to distinguish their rearing parent's contact calls from non-parent contact calls with no distinction between male and female parents, suggesting that the contact call possesses one or more parameters that the nestlings recognize. Although nestlings responded preferentially to their parents, Leonard et al. (1997b) did not find that parents responded preferentially to their own young. It is possible that parents are able to recognize their offspring just prior to fledging, at 18-22 days (Robertson, Stutchbury& Cohen 1992), which is slightly older than the mean age (15.7 days) of the nestlings used in Leonard et al. (1997b)'s study. However, it is unlikely that the nestling call changes in the last few days prior to fledging in such a way that would make it more recognizable to the parent(Andy Horn, unpublished observation).

Despite the evidence that parent tree swallows may not recognize their offspring, the evidence that nestling tree swallows recognize their parentssupports investigating the design and ontogeny of a parent-offspring recognition mechanism in tree swallows.

2.2 Vocal learning and vocal convergence

Vocal learning, which Tyack (2008) defines as "the ability to modify the acoustic structure of a vocalization based on auditory input" (319), is one theory of how parents and offspring develop recognition for one another. Sharp &Hatchwell (2005) found that the "churr" call of nestling long-tailed tits (*Aegithaloscaudatus*) raised by foster parents was more similar to the churr call of their foster parents than that of their genetic parents, suggesting that the nestlings learned the call from their parents. This mechanism of learning, where the calls of individuals in a distinct group become more similar to each other over time, is called vocal convergence. Call convergence can be advantageous for many different reasons, from improving communication in noisy environments and maintaining contact between individuals, to strengthening social bonds and promoting recognition mechanisms (Mundinger 1970; Tyack 2008). Convergence-based recognition mechanisms, where the receivers and senders in an associated group of individuals rely on one "converged" cue, are simpler than mechanisms that rely on senders and receivers producing and recognizing multiple individually-distinct cues in the group. This single, converged cue may reduce the rate of error in recognition, making it more reliable than the multiple-cue mechanism.Thus, we expect that nestlings will converge components of their calls with the calls of their parents.

2.3 Genetic inheritance and vocal learning of parent-offspring call similarities

One of the strongest counter-arguments to a learning-based parent-offspring recognition mechanism is for offspring to inherit a phenotype from their parents that becomes therecognition cue. In this case, similarities between the calls of offspring and parents result from the inheritance of structural and behavioural phenotypes, rather than from learning. The balance between learned and inherited vocal components, however, can vary within a species. The vocalizations of cliff swallow chicks (*Hirundopyrrhonota*), a colonial species, seem to be genetically inherited rather than learned, although the authors stressed that the study was perhaps not strong enough to distinguish between pure genetic influence and a mixture of genetic and learned influences (Medvin, Stoddard & Beecher 1992). Also, Forstmeier et al. (2009) observed that female zebra finches (*Taeniopygiaguttata*) did not learn any of the investigated components of their distance calls, while males learned components of their calls from both the male adults who raised them and peer group members. Thus, learned and genetic components might both be present in offspring vocalizations.

Genetically determined cues are not always reliable as recognition cues. Genetic recombination, for example, can distort the similarities between offspring and parent calls (Beecher 1988). Tree swallows have the additional issue of extra-pair fertilizations; a female can copulatewith her pair male and several other males outside her pair, so the offspring the pair feed and brood can have several fathers. Extra-pair fertilizations are frequent in some tree swallow populations (57-80% of broods) (Lifjeld et al. 1993; Dunn et al. 1994), suggesting that a strong genetic component in a tree swallow recognition mechanism would be disadvantageous. Furthermore, the male parent tends to vocalize

more than the female parent during the early nestling stages of offspring development (Leonard, Fernandez & Brown 1997a). This suggests that the male parent relies strongly on vocalizations when provisioning food, although the reason for this large number of male calls is unknown and could be for some other purpose (e.g. to communicate with the female rather than with nestlings, Leonard Fernandez & Brown 1997a). Because extra-pair fertilizations result in the male parent being unrelated to some of the offspring, having a strong genetic component in the recognition mechanism would increase recognition errors in tree swallow parent-offspring interactions. For these reasons, it is expected that the parent-offspring recognition mechanism for tree swallows has a stronger learned component than genetic component.

2.4 Reproducibility of the study

It should be noted that the specific population of tree swallows used for this study behaved more as anaggregation than as solitary pairs, as they nested in close proximity to one another,and were observed engaging in social behaviour throughout the breeding season, including feather chasing (Weydemeyer 1934), brief synchronous departures from the nest ("towering", Kuerzi 1941) and predator mobbing (Robertson, Stutchbury& Cohen 1993). Because of the relatively high degree of colonial behaviour, this population of tree swallows may have a greater selection for parent-offspring recognition mechanisms than solitary pairs. Future reproductions of this study should therefore consider the degree of colonial behaviour of their study subjects, as it may influence the results.

2.5Delimitations of the literature

The primary source for literature was a collection of published journal articles created by Andy Horn and Marty Leonard of Dalhousie University, and HendrikReers of the Max Planck Institute for Ornithology inSeewiesen, Germany. This collection included all papers authored by A. Horn and/or M. Leonard, and papers that are relevant to or referenced in their past and current research. Secondary searches for published journal articles were done using ScienceDirect and Google Scholar, using key words "call/vocal learning", "vocal convergence", "vocal inheritance", "tree swallow", "call similarity" and "call individuality/individual distinctness".

3.0 Methods

This section outlines the procedural and analytical methods of the project. It begins with a description of the study site and a brief statement of the research design andsampling method. It then describes the procedures employed in the fieldand the proposed acoustic and statistical analyses of the call data. It finishes with a work schedule for the remaining components of the project.

3.1 Study site

The tree swallows used for this study come from a population that nested at four sties in the Gaspereau Valley near Wolfville, Nova Scotia, Canada from late April to early July, 2010 (Figure 1, 2). All four sites consist of a mixture of open field and overgrown apple orchard. Nest boxes were placed every 10 m around the perimeter of the fields in sites B, C, and D. In sites A and D, nest boxes were placed within the orchards, spaced roughly 20 m apart in grids (Leonard & Horn 1996). The sampling of these sites

was opportunistic, as the nest boxes were already established from research in previous

years, and the sites were known to support a reliable population of tree swallows.

Figure 1. Map of Nova Scotia, showing town of Wolfville approximately 100 km North-West of Halifax. Map retrieved from http://maps.google.ca/maps?hl=en&tab=wl, December 6, 2010.

3.2 Study design

The research design is a cross-fostering experiment. The objective of the design is

to change the rearing association between parents and offspring from genetic to non-

genetic. This allows for data analysis that correlates nestling calls with calls of genetic

and non-genetic parents. Data collection occurred in Wolfvillebetween May 12th and July

6th, 2010.

Figure 2. Location of study region(red box) in relation to Wolfville, Nova Scotia. Specific study sites within the study region are shown in figure 3. Satellite images in figures 2 and 3 were retrieved from http://maps.google.ca/maps?hl=en&tab=wl, December 6, 2010.

Figure 3. Study sites (red boxes A, B, C, D) within the study region (see figure 2). The Gaspereau River is the dark winding line that runs adjacent to sites B and C. Sites A, B and D were a mixture of overgrown apple orchard and open field. Site C was a mixture of open field and riparian habitat.

3.3 Sampling design

The nest that parents and nestlings belong to is the unit of analysis, for two

reasons. First, individual nestlings within a nest are not statistically independent points,

because they are raised together and may influence the structure of each other's calls (Leonard & Horn 2001b). Second, the average call of all nestlings in the nest gives a better estimate of overall similarity than comparing each nestling separately. The sample size is 16 nests chosen from the 65 tree swallow "nest box" nests within the four sites. The study is restricted to these nests because they hatched latest in the field season, when there was more time to record older nestlings (see section 3.9 Limitations and delimitations).

3.4 Cross-fostering experiment

Cross-fostering techniques, where infants are removed from their genetic parents and raised by unrelated foster parents (Mateo & Holmes 2004), are often used for research on kin recognition. The foster design of this study is called a nonreciprocal cross-fostering design. It is useful because nestlings are exposed to the cues of a nonrelated foster parent. One disadvantage of the design is that nestlings are exposed to vocal cues of unrelated foster siblings, and these cues may influence the nestling call and mask components learned from the foster parent. This method was chosen because the study is part of a larger project that required a nonreciprocal design.

The cross-fostering experiment has a sample size of 10 nests. The only criterion that decided whether the nest was experimental or control was the hatching synchrony with other nests of similar brood size. All nests in one swap must hatch on the same day or within 2 consecutive days of each other, and must not differ in brood size by more than 1-2 nestlings. This was to ensure foster parents were raising a brood similar to their original brood. The 6 nests that had no other nests of similar age available for swaps were left alone, as controls, with nestlings raised by their original pair of parents.

The experiment consisted of four nestling "swaps".Swaps occurred when nestlings were 3-4 days old, oncethey were big enough to be handled and had minimal vocal development.Each swap included three nests with at least four nestlings per nest. For each nest, the brood was divided into two halves of roughly equal total weight, and each half was sent to one of the two other swap nests. It was necessary to sortthe nestlings by weight, in case size influenced call structure; a nest of all the heaviest nestlingsmay sound significantly different from a nest of all the lightest nestlings, which were sometimes relatively underdeveloped. This was achieved as follows. First, all nestlings within a nest were weighed and ranked by weight from heaviest (rank 1) to lightest. The nestlings were then divided between odd numbered ranks (e.g. 1,3,5) and even numbered ranks (e.g. 2,4,6). Nestlings were given markings on their toes with a Staedtler® Lumocolor permanent marker (non-toxic) that identified the brood they came from and their rank. During the swap, the odd-ranked nestlings went to one nest and even ranks went to the other nest. When the swap was completed, each nest had a set of odd ranks from one nest and a set of even ranks from the other (figure 4).

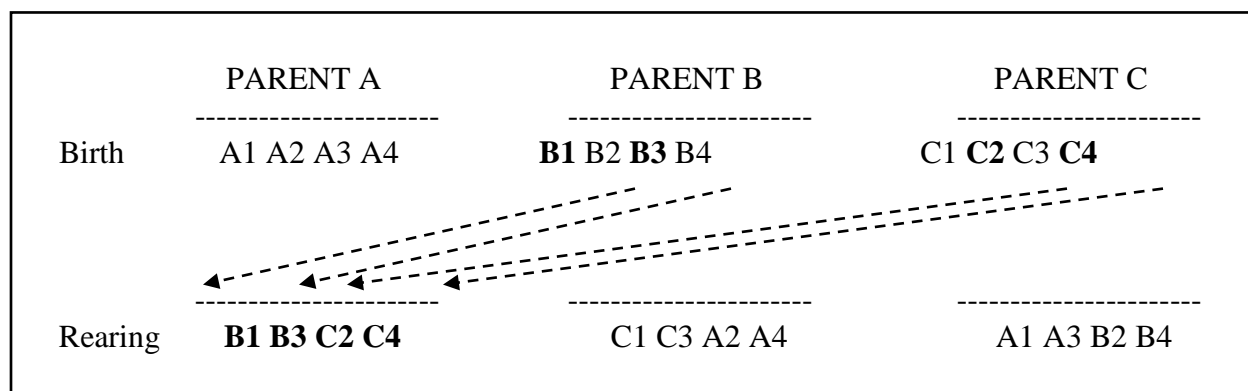|	PARENT A	PARENT B	PARENT C
Birth	A1 A2 A3 A4	**B1** B2 **B3** B4	C1 **C2** C3 **C4**
Rearing	**B1 B3 C2 C4**	C1 C3 A2 A4	A1 A3 B2 B4

Figure 4. Diagram of nonreciprocal cross-fostering design, adapted from Mateo & Holmes (2004). Nestlings are represented by the letter of their birth parent and their weight rank, for example A1 is the heaviest nestling born in parent A's nest. The nestlings in bold (B1, B3, C2, C4) and the arrows represent how nestlings are assembled into their rearing nest.

3.5 Recording parent calls

Parent calls wererecorded when the nestlings were 4-12 days old, because parents tend to call when the nestlings are younger (Leonard, Fernandez and Brown 1997a). Calls were recorded using AKG C417 tie-clip microphones and an M-AUDIO Micro-track II mobile digital recorder. Parents tend to vocalize both inside and outside the nest box, depending on the sex of the parent and the life stage of the nestlings (Leonard, Fernandez and Brown 1997a). To record calls inside and outside the nest box, two microphones were clipped onto the box: one insidehanging 10-15 cm above the nestlings, and the other outside hanging 5 cm above the nest box entrance. Anobserver watched the nest through a Swarowski ATM 80 mm spotting scope from a distance of 10-20 m, andnoted the time when parents entered and left the nestbox. Each recording lasted at least 30 minutes. If parents did not enter the nest box more than twice during the 30 minutes, the recording was either extended until the parents returned or the nest was recorded again at a later date.

The sex of each parent was determined whenever possible when parents entered and exited from the nest box. Female adults under 2 years of age are easily distinguished frommaleadults, because they have more brown, dullplumageon their backs than males. Females were also distinguishablefrom males if they werecolour-banded, as any brooding females found in the nest boxduringnest checkswere checked for bands.In terms of confidence of parent sex determination, 12 nests had moderate (e.g. one parent had a duller upper-sidecolour) to high (e.g. female was banded orone parent clearly had first-year female plummage) confidence of sex determination, while 4 nests had low confidence (e.g. vague colour difference) to unknown sex determination.Four nests

recorded only the male parent, 3 nests recorded only the female parent, 6 nests recorded both male and female parents, 2 nests recorded both parents of undetermined sex, and 1 nest recorded one parent of undetermined sex.

3.6 Recording nestling calls

Nestlings were banded and their throat feathers coloured using Staedtler® Lumocolor permanent marker when they were 13-15 days old. Nestlings werecoloured within this time frame because they had enough feathers to colour, but were too underdeveloped to fly away if agitated. Each nestling in the nest received a different throat colour, and the toe markings were documented so the original nest of each nestling was known.

Nestling calls were recorded 18-21 days after hatching. At this age, nestlings sit at the nest opening to be fed by parents. Nestlings stay at the opening until they are pushed back into the nest by another nestling, usually after a few minutes, so it is possible to record many different nestlings at the nest opening.Calls were recorded using aSennheiser® shotgun microphone placed approximately 1 m from the nest box entrance, to avoid disturbing nestlings and causing premature fledging. The microphone was attached to a tripod and pointed at the nestbox entrance.The observer watched the nest from a distance of 10-20 m through the scope and noted when the nestling occupied the nest opening, the throat colour of the nestling, feeding events, and other activity at the nest. Recordings typically lasted 30-40 minutes. If no more than half the nestlings in the nest sat at the hole during the recording, the recording was repeated later in the day or the following day.In total, 60 nestlings were recorded from the 16 nests, with an average of 3-4 nestlings recorded per nest.

3.7 Call analysis

The nestling or parent producing each call was identified from observer notes made during recording. All nestling begging calls and parent contact calls that were free from background noise were removed from the original recording using Audacity 1.3.12-beta software.One to twenty-five calls were chosen for analysis per nestling(mean±sd: 10.2±5.8, range: 1-25), depending on the number of calls each nestling made. One to ten calls were chosen for analysis per adult (mean±sd: 3.1±2.8, range: 1-10), also depending on the number of calls each adult made.

All calls were analyzed using Sound Analysis Pro® 2.063 software, which measures multiple acoustic features of a call simultaneously (Tchernichovski,Swigger &Mitra 2004).The call parameters analyzed for this study include call duration, frequency modulation, entropy and mean frequency. Call duration in measured in milliseconds (ms). Frequency modulation is derived from the amount frequency varies away from constant frequency over time, where low modulation indicates a pattern closer to a constant frequency and high modulation indicates more variation. Entropy is a measure of spectral width, where low entropy values are more tonal/pure and high entropy values are more harsh/noisy. Mean frequency is measured in Hertz (Hz) (Tchernichovski,Swigger &Mitra 2004). These parameters were chosen because they are referenced as evidence of vocal similarity in past and current research on tree swallows (Leonard et al. 1997b; HendrikReers, personal communication), and frequency and duration are often individually distinctive parameters in calls of other bird species (Sharp &Hatchwell 2005; Mammen&Nowicki 1981).

After all calls were analyzed, mean call parameters were calculated for all nestling and parent individuals. Nestlings were then grouped by a) nest of rearing, b) nest of origin and c) control nest, and the mean parameter values for each nest were calculated from the nestling means.

3.8 Pearson product-moment correlation coefficient

The statistical parameter used to analyze the data is the Pearson product-moment correlation coefficient (denoted as *r*). The correlation coefficient is an index for the strength of the linear relationship between two continuous random variables (Lockheart 1997, p. 596). In other words, *r* describes the amount of variation in the continuous variable 'x' (i.e. the parent call parameters) that correlates with the variation in the continuous variable 'y' (i.e. the nestling call parameters). *r* is scaled between 0 and 1, where 0 implies no linear relationship, and 1 implies a perfect linear correlation.

All correlations were tested for significance using a *p*-value, where α=0.05 for significant results. If the nest call parameter value is similar to the parent call parameter value, *r* will be closer to 1 and *p* will be ≤0.05. If the nest call parameter value is not similar to the parent call parameter, *r* will be close to 0 and *p* will be >0.05. It is also important to note that significant negative relationships between parent and nestling calls do not support the hypothesis that parent and nestling calls are similar, because a negative relationship implies that parent and nestling parameters are inversely proportional, where a positive relationship implies that they are directly proportional. Therefore, only positive significant relationships support the hypothesis.

The *p*-value assumes that the data points are normally distributed, therefore it was necessary to assess the data for normality. Histograms for all four parameters, which

plotted parameter value on the x-axis versus nestling count on the y-axis, revealed

visually that nestling calls exhibit a strong normal distribution in for all four call

paramters. Although there were not enough calls to replicate this technique for parents,

the normality of the nestling calls is assumed to infer normality for parent calls as well.

All of the statistical data analysis was completed with the statistical software

program R, version 2.12.2.

3.9 Statistical analysis design

There are three parent-nest comparisons between nestling and parent that were

tested for linear correlations, one for control nests and two for the cross-fostered nests:

1) Control nest – parent vs. genetic offspring

2) Cross-fostered nest – i) parent vs. genetic offspring,

i.e. offspring from brood before cross-fostering

ii) parent vs. fostered offspring,

i.e. offspring raised after cross-fostering

For each comparison, the parent parameter value is plotted on the horizontal axis and the

nest value (i.e. the mean value for all the nestlings in a nest group) is plotted on the

vertical axis. The intersection of those values is the data point. We hypothesized that call

learning has a stronger influence than genetics on vocal similarity between parents and

offspring. Therefore, we predicted that the control and foster correlations would be

stronger than the genetic correlations. This was verified from the 95% confidence

intervals of the correlation coefficient. If learning plays a more significant role in parent-

offspring call similarity than inheritance, the confidence interval for the "learning" *r-*

value would be closer to 1 than the "genetic" r-value confidence intervals, and the confidence intervals for those values would not overlap.

Male and female parents were first tested separately against nest values (figure 5), because the male and female parents in the nest pair are assumed to produce individually distinct calls, and therefore each parent may influence nestling calls differently. However, because there were not enough male and female calls from the control nests for significant control results, an additional comparison between nestling calls and parent calls (no distinction between male or female) was necessary. In these comparisons, some nests have two data points, one for male and one for female, where both male and female parents for that nest were recorded.

In total, we conducted 28 parent-nestling comparisons. In terms of male and female parent calls, this includes 4 comparisons (duration, frequency modulation, entropy and mean frequency) between female call parameters and nest of rearing parameters, 4 comparisons between female parameters and nest of origin parameters, 4 comparisons between male parameters and nest of rearing parameters and 4 comparisons between male parameters and nest of origin parameters (figure 5). In terms of parent calls with no sex determination, this includes 4 comparisons between parent call parameters and nest of rearing parameters, 4 comparisons between parent parameters and nest of origin parameters, and 4 comparisons between parent parameters and control nest parameters (figure 5).

3.10 Limitations and delimitations

The major limitations to this study were time constraints imposed by the larger project the study was a part of. The primary objective of the larger study was to record

nestlings from 65 nests when they were 8-9 and 12-13 days old, and there was less time allotted for recording older nestlings. Data collection was also limited by the brief, and sometimes unpredictable, window of opportunity for recording nestlings at the nest opening before fledging, usually only 2-3 days.

The sample is limited to tree swallows from these four Wolfville sites, because nest boxes had been erected at these sites during past research projects.Therefore, these sites were both a reliable and feasible source of study subjects. The data is limited to recordings of nestlings at least 18 days of age and does not include nestlings at days 8-9 or 12-13. This is because the oldest nestlings have the most developed vocalizations, and are the most likely to exhibit acoustic similarities to their parents.

4.0 Results

Section 4.0 presents the results obtained from the study methods described in section 3.0. The section begins with a summary of the main results, followed by the supporting figures and data tables. Appendix A (p.49)contains a larger version of the graphs in figure 5 (p.29), so that they may be studied more closely if readers find figure 5 difficult to read.

4.1 Call similarity between parent contact call and nestling begging calls

Of the 28 linear relationships tested, only one parent-nestling comparison has a positive correlation coefficient with $p \leq 0.05$. This exception is male parent frequency modulation versus nest of rearing frequency modulation (r=0.82, p=0.05; figure 5-K, table 1). Parent duration versus nest of rearing duration also had a p-value below 0.05 (r=-0.57,p=0.03; figure 6-A, table 2), however because this relationship is negative, the result does not support the hypothesis that parent calls and offspring calls are similar.

Therefore, the majority of the evidence suggests that there is no relationship of similarity between parent calls and the calls of nestlings they reared, the calls of nestlings they hatched, or the calls of control nestlings, which were both hatched and reared by the same parents.

4.2 Effects of female and male parent calls on nestling calls

All of the correlation confidence intervals for female parent comparisons and male parent comparisons overlap (table 1). This indicates that neither male nor female parent call parameters better explain the variation in nestling call parameters. Furthermore, because all confidence intervals overlap, the significance of the correlation between male parent frequency modulation and nest of rearing frequency modulation is lessened. Therefore, it is possible that none of the comparisons, including male versus rearing frequency modulation, yielded significant correlation coefficients.

4.3 Effects of learning and inheritance on nestling call parameters

All of the confidence intervals for comparisons between parent parameters and nest of rearing parameters, nest of origin parameters and control nest parameters overlapped (table 2). Therefore, there is no evidence to support a vocal convergence mechanism or a genetic inheritance mechanism of similarity in tree swallows. This result suggests two additional conclusions. First, the experimental results suggest that neither the effects of learning nor the effects of inheritance have a greater effect on nestling call structure, such that the nestling call would be similar to the parent call. Second, the control results suggest that the combined effects of learning and inheritance do not result in call similarity, nor do they have a greater effect on nestling call structure than learning or inheritance would alone.

4.4 Figures and tables

Section 4.4 contains the figures and tables referenced above. These begin on the following page, p.29.
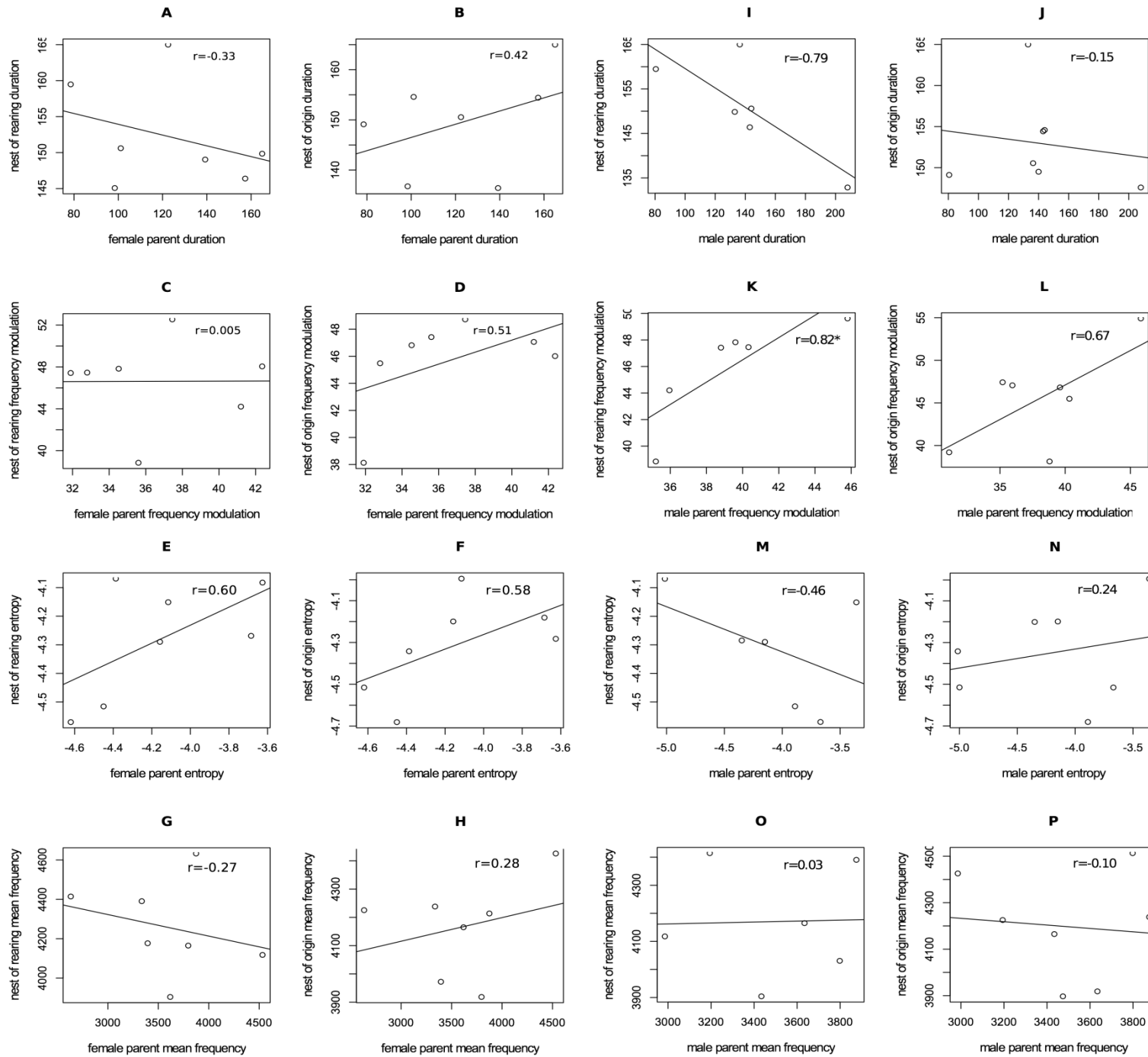
Figure 5. See p.30 for figure caption. See appendix A for graphs at a larger scale.

Figure 5 (*see p.29 for graphs*)**.**Associations between male and female contact call parameters (females: figures 4A-4H, males: figures 4I-4P) and the mean nestling begging call parameter values from nest of rearing and nest of origin. 'r' is the Pearson product-moment correlation coefficient of the association, where '*' refers to r values with $p \leq 0.05$ (adapted from Ezenwa et al. 2006). Note that the line contained in each graph is meant as a visual aid, and does not represent the linear relationship implied by the correlation coefficient. *A)* Female parent duration (DUR) versus nest of rearing DUR. *B)* Female parent DUR versus nest of origin DUR. *C)* Female parent frequency modulation (FM) versus nest of rearing FM. *D)* Female parent FM versus nest of origin FM. *E)* Female parent entropy (EN) vs nest of rearing EN. *F)* Female parent EN versus nest of origin EN. *G)* Female parent mean frequency (MFQ) versus nest of rearing MFQ. *H)* Female parent MFQ versus nest of origin MFQ. *I)* Male parent DUR versus nest of rearing DUR. *J)* Male parent DUR versus nest of origin DUR. *K)* Male parent FM versus nest of rearing FM. *L)* Male parent FM versus nest of origin FM. *M)* Male parent EN vs nest of rearing EN. *N)* Male parent EN versus nest of origin EN. *O)* Male parent MFQ versus nest of rearing MFQ. *P)* Male parent MFQ versus nest of origin MFQ.

Table 1. Associations between female and male contact call parameter values and mean nestling begging call parameter values from nest of rearing and nest of origin. 'r' is the Pearson product-moment correlation coefficient for each association, 'p' is the *p*-value for the coefficient and the 95% confidence interval is also for the coefficient. The significant *p*-value is in bold, assuming $\alpha = 0.05$.

| nest call parameter	correlation with female parent call parameters	95% confidence interval	correlation with male parent call parameters	95% confidence interval
nest of rearing duration	r = -0.33 p = 0.47	-0.86 – 0.56	r = -0.79 p = 0.06	-0.98 – 0.05
nest of origin duration	r = 0.42 p = 0.35	-0.49 – 0.89	r = -0.15 p = 0.74	-0.81 – 0.68
nest of rearing frequency modulation	r = 0.005 p = 0.99	-0.75 – 0.76	r = 0.82 **p = 0.05**	0.03 – 0.98
nest of origin frequency modulation	r = 0.51 p = 0.24	-0.39 – 0.91	r = 0.67 p = 0.10	-0.17 – 0.94
nest of rearing entropy	r = 0.60 p = 0.16	-0.29 – 0.93	r = -0.46 p = 0.35	-0.93 – 0.56
nest of origin entropy	r = 0.58 p = 0.17	-0.31 – 0.93	r = 0.24 p = 0.60	-0.62 – 0.84
nest of rearing mean frequency	r = -0.27 p = 0.56	-0.85 – 0.61	r = 0.03 p = 0.96	-0.80 – 0.82
nest of origin mean frequency	r = 0.28 p = 0.54	-0.60 – 0.85	r = -0.10 p = 0.83	-0.79 – 0.71
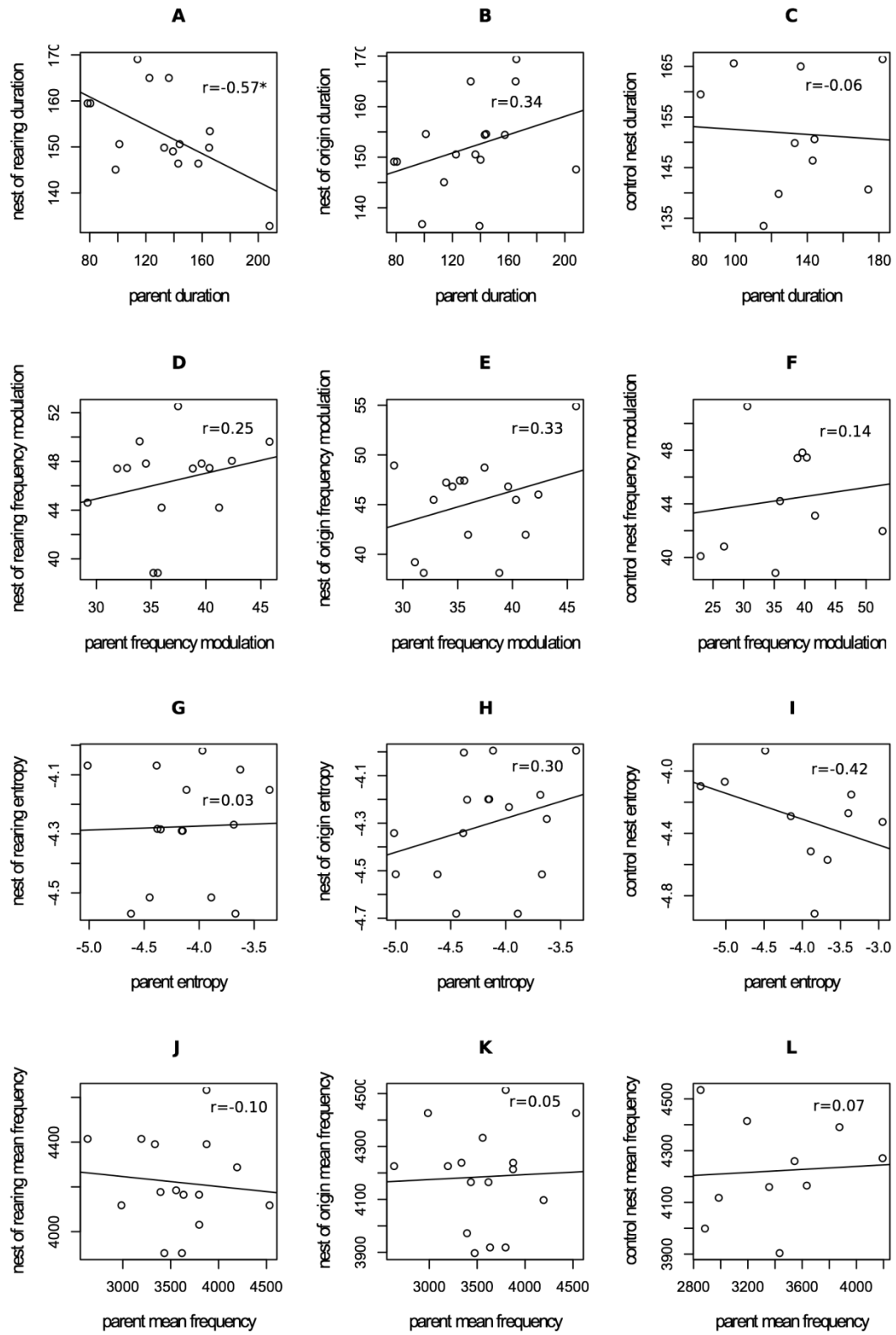
Figure 6. See p.32 for figure caption.

Figure 6 *(see p.31 for graphs).* Associations between parent contact call parameters (no distinction between male, female and unknown) and mean nestling begging call parameter values from nest of rearing, nest of origin and control nest. See figure 1 (p.29) for further details. *A)* Parent DUR versus nest of rearing DUR. *B)* Parent DUR versus nest of origin DUR. *C)* Parent DUR versus control nest DUR. *D)* Parent FM versus nest of origin FM. *E)* Parent FM vs nest of rearing FM. *F)* Parent FM versus control nest FM. *G)* Parent EN versus nest of rearing EN. *H)* Parent EN versus nest of origin EN. *I)* Parent EN versus control nest EN. *J)* Parent MFQ versus nest of rearing MFQ. *K)* Parent MFQ versus nest of origin MFQ. *L)* Parent MFQ versus versus control nest MFQ.

Table 2. Associations between parent contact call parameter values (no sex determination) and mean nestling begging call parameter values from nest of rearing, nest of origin and control nest. 'r' is the Pearson product-moment correlation coefficient for each association, 'p' is the *p*-value for the coefficent and the 95% confidence interval is also for the coefficient. The only significant *p* value is in bold, assuming $\alpha=0.05$.

nest call parameter	parent call parameter	95 % confidence interval
nest of rearing duration	r = -0.57 **p = 0.03**	-0.84 – -0.08
nest of origin duration	r = 0.34 p = 0.20	-0.19 – 0.71
control nest duration	r = -0.06 p = 0.86	-0.67 – 0.59
nest of rearing frequency modulation	r = 0.25 p = 0.37	-0.30 – 0.67
nest of origin frequency modulation	r = 0.33 p = 0.22	-0.20 – 0.71
control nest frequency modulation	r = 0.14 p = 0.70	-0.54 – 0.71
nest of rearing entropy	r = 0.03 p = 0.91	-0.49 – 0.53
nest of origin entropy	r = 0.30 p = 0.26	-0.23 – 0.69
control nest entropy	r = -0.42 p = 0.23	-0.83 – 0.29
nest of rearing mean frequency	r = -0.10 p = 0.71	-0.58 – 0.43
nest of origin mean frequency	r = 0.05 p = 0.87	-0.46 – 0.53
control nest mean frequency	r = 0.07 p = 0.85	-0.59 – 0.67

5.0 Discussion

Section 5.0 discusses the results presented in section 4.0. It first addresses the lack of call parameter similarity between parent and nestling calls, and the implications of the result on parent-offspring recognition. This is followed by a discussion of the effects of male and female parent calls on nestling calls, and a discussion of the effects of learning and inheritance on nestling calls, both in the context of recognition. These three sections lead into a case study, which uses two key studies to discuss the role of call similarity and call individuality in parent-offspring recognition. Section 5.0 concludes by stating some of the crucial assumptions made in this study.

5.1 Lack of call similarity between parent and nestling calls

The contact calls of tree swallow parents were not significantly similar to the mean begging calls of their nestlings in terms of duration, frequency modulation, entropy or mean frequency. This was a consistent result in all comparisons between control nestlings and their parents, cross-fostered nestlings and their rearing parents and cross-fostered nestlings and their original parents. Similarly, there was no significant difference between comparisons for male parents and for female parents. These results do not support the hypothesis that nestlings would have call parameters that were similar to the call parameters of their parents, as part of a nestling-parent recognition mechanism. It may be that tree swallows do not use a parent-offspring recognition mechanism. This could be because they are only a semi-colonial species (Robertston, Stutchbury and Cohen 1993), and, as this implies that tree swallows frequently nest in solitary pairs, there is less selection for a mechanism that distinguishes family groups from other family groups. However, because Leonard et al. (1997b) found that older nestling tree swallows

called more to their true parent's contact call, there is external evidence that a tree swallow parent-offspring recognition mechanism is in place.

It is important to note that the results do not contradict the presence of a recognition mechanism in tree swallows. There is a lack of evidence for a two-way recognition mechanism, where parents and nestlings recognize each other by sending and receiving the same cue. Instead, the mechanism may only work one way, where nestlings recognize their parents but parents do not recognize their nestlings. Leonard et al. (1997b) found that the parent tree swallows did not discriminate between the playback calls of true offspring and non-offspring, which suggests that parents do not recognize the vocal cues of their own offspring. This form of non-reciprocal recognition between nestlings and parents may be consistent with the results of this study. If parents are unable to recognize their own young by their calls, then there is no advantage to a nestling who sounds similar to its parent. It may still be advantageous for the nestling to learn and recognize its parent call for the purpose of locating the parent after fledging(Beecher 1981), however the nestling may do this without converging with the parent call.

Another factor that may explain the lack of similarity between nestling and parent calls is the presence of individually distinctive calls in tree swallows. The calls of nestling tree swallows 15-20 days of age (just prior to fledging) have been found to differ significantly between individuals, both in terms of a few specific parameters (duration, initial frequency, frequency range; Leonard et al. 1997b) and, for the nestlings recorded in this study, in terms of several weighted parameters(Reers 2011). Individual distinctiveness is very important to many social animal species, not just for offspring

recognition, but also for other mechanisms such as mate recognition, territorial behaviours, and social hierarchies (Pollard & Blumstein 2011). Tree swallows in particular may be selected for individually distinctive calls in communication between adults, especially between nesting pairs (Roberston et al. 1992, Leonard et al. 1997b). In the context of this study, nestlings that avoid sounding like their parents may have an added advantage in that they are able to develop individually distinctive calls at an early age without running the risk of sounding too much like their siblings.One argument against this is that tree swallow nestlings have been found to converge vocally with siblings (Leonard & Horn 2001b, Reers 2011). This sibling call similarity, however, is hypothesized to increase the overall feeding rate to the brood by sending a stronger, uniformed brood signal to parents, especially since it is most pronounced when nestlings call together (Leonard & Horn 2001b). Thus, when nestlings leave the nest and are calling to parents on their own, siblings are no longer able to converge their calls, the brood signal disappears, and any advantage of sibling call similarity to a potential recognition mechanism is lost.Therefore, it is possible that tree swallow nestlings do not sound similar to their parents because it confers no advantage to parent-offspring recognition, and, because of sibling-sibling call convergence, it avoids over-convergence among siblings.

5.2Effects of male and female parent calls on nestling call parameters

Overall, neither male nor female parent calls were more significantly correlated with nestling calls from the experimental nests of rearing or nests of origin. The lack of significant correlations between male and female parent calls and nest of origin calls suggests that inherited similarities are minimal, perhaps due to recombination and extra-

pair copulation (see section 5.3 for discussion). The only significant correlation was between male parent frequency modulation and nest of rearing frequency modulation (table 1), which may support the presence of a learning mechanism. However, call entropy and mean frequency showed non-significant correlations, and although male parent duration is significantly correlated with nest of rearing duration, the relationship is negative and thus non-significant (figure 5). Therefore, because of the non-significant correlations of the other call parameters, it is unclear whether this significant frequency modulation correlation indicates a true causal link between the male parent and the nestlings he rears.

Nestlings may not preferentially converge with the call of either the male or female parent because they have no way of distinguishing whether the calls they hear in the nest come from the male or female parent. It is unlikely that nestlings combine the individually distinct parameters in parent vocalizations with the time or situation when those vocalizations are heard to distinguish between the male and female parent. This is because both parents call to them in the nest during feeding events, and females tend to call less when they visit the nest for brooding, which is the only parent-nestling interaction that females are suspected to do more than the males (Leonard, Fernandez & Brown 1997a;Robertston, Stutchbury and Cohen 1993). If nestlings do converge with their parent calls, it is therefore most likely that they converge with the parent who calls to them the most, rather than the parent that they identify as male or female. Leonard, Fernandez & Cohen (1997a) found that male tree swallows called more overall at the nest box than female tree swallows, females called more inside the nest box beside the nestlings than outside, and males called most often outside the nest box, perhaps to

communicate with the female parent rather than with nestlings. This suggests that both parents communicate equally overall with nestlings, therefore, nestlings have no mechanism to preferentially learn either the male or female call. The lack of evidence that males call more to the nestlings than females, coupled with the findings that nestling calls were not more or less similar to either parent, suggests that nestlings do not converge either the male or female parent for recognition purposes.

Once again, it is important to note that these results do not suggest nestlings are unable to recognize their parents' calls. In fact, the literature supports the opposite scenario, where nestlings can recognize both the male parent and female parent calls. Leonard et al. (1997b) found that nestlings begged more to their true parents' calls than to other adult calls, and furthermore nestlings responded similarly to the calls of both the male and female true parent. Those findings suggest that nestlings are able to recognize both the male and female parent calls, perhaps because of the significant individual variation among adult contact calls (Leonard et al. 1997b). This idea supports the importance of call individuality in tree swallow communication, and further suggests that call individuality, not call similarity, plays the more important in a non-reciprocal parent-offspring recognition mechanism. In such a mechanism, there would likely be selection for individually distinct adult calls, as this would improve the nestling's ability to distinguish its parents from other parents in the colony.

5.3 Effects of learning and inheritance on nestling call parameters

Parent calls, when the sex of the parent is ignored, were not significantly positively correlated with control nests, nests of rearing or nests of origin for any of the call parameters. There was also a complete overlapping of correlation coefficient 95%

confidence intervals for all parent-nestling comparisons of all four parameters. Furthermore, control nest coefficients were not found to be more similar to comparisons of experimental nestlings and their rearing parents, nor experimental nestlings and their original parents. These results suggest that there is no difference between the effects of learning and the effects of phenotype inheritance on nestling call parameter values. Therefore, there is no evidence to support the hypothesis that learning recognition cues based on call similarity may be more reliable than inheriting recognition cues based on call similarity. It is noted once more that the results do not undermine the presence of a recognition mechanism in tree swallows. Rather, the results do not support the hypothesis that tree swallows use a recognition mechanism based on call similarity between nestlings and parents, either learning-based or genetically derived, which would allow nestlings and parents to be both the receivers and senders of one common signal: the parent call.

There is a key difference between recognition mechanisms that are based on inherited recognition cues and mechanisms that are based on learned recognition cues. Genetically derived recognition mechanisms inherently rely on call similarity between nestling and parent, because the shared genes between parents and nestlings create phenotypic similarities that allow for self-matching (Mateo 2010). The lack of a significant correlation between parent calls and nest of origin calls undermines the presence of this mechanism. Learning-based recognition mechanisms, on the other hand, may (Sharp et al. 2005) or may not (Hughes, Nowicki&Lohr 1998) be based on call similarity. Mechanisms that are not based on call similarity may be expected to occur where senders and receivers do not have reciprocal roles. In the context of parent-

offspring recognition, this may be where nestlings (as receivers) recognize the calls of parents (as senders), but parents (as receivers) cannot recognize the calls of nestlings (as senders). Because recognition only goes one way, the advantage of call similarity, which allows parents to self-match their call to the cue received from nestlings, is negligible. Because this one-way recognition between nestlings and parents is what Leonard et al. (1997a) found evidence for in tree swallows, our results may support the hypothesis that tree swallows use a recognition mechanism that does not rely on call similarity.

5.4 Learning-based recognition mechanisms: call similarity versus individual distinctiveness

Two specific studies have found evidence of a learning-based parent-offspring recognition mechanism. One study found evidence of call similarity in the recognition mechanism, while the other found evidence of individual distinctiveness in the mechanism. By discussing these twostudies, it is possible tohypothesize why call similarity may not play a strong role in a tree swallow offspring-parent recognition mechanism.

Sharp et al. (2005) measured the call parameters of nestling and parent long-tailed tits (*Aegithaloscaudatus*) after conducting a cross-fostering experiment similar to this study. They found that the nestling calls were more similar to their rearing parents (male and female) than to their true parents, suggesting that nestlings learn the calls of their parents after hatching in order to sound similar to the provisioning adults. Long-tailed tits differ from tree swallows in that they breed cooperatively, where helper adults separate from the brood pair provide for young that are closely related to them (Sharp et al. 2005, Hatchwell et al. 2004). The added benefit of cooperative provisioning applies selective pressure for nestlings that are able to imitate the cues of the provisioning adults (Beecher

1988). Although nestlings are attempting to imitate adults that are genetically related to them, genetic recombination could alter the similarities between calls, whereas the consistent nest environment where nestlings are raised offers good evidence of kinship (Beecher 1988, Sharp et al. 2005). Tree swallows have not displayed evidence of helpers in their social structure, therefore there may be less selective pressure on tree swallows to use cue-similarity based recognition mechanisms.

An important alternative to similarity-based recognition may be recognition that does not rely so heavily on imitation. Receivers may learn cues and associate those cues with their senders, however the original receivers (new senders) will not send the same cue back to the original senders (new receivers) if and when the roles are reversed. Hughes, Nowicki and Lohr (1998) attempted to show that recognition cues between nestling and parent black-capped chickadees (*Poecileatricapillus*) can develop from more than simple imitation. Using the "chick-a-dee" calls of wild chickadees as the definition of "normal" chickadee calls, the authors found that chickadees raised in the lab with extensive social and vocal interaction with adult birds produced call notes that were more similar to wild chickadee notes than were the notes produced by chicks raised with less adult interaction. However, some of the call notes produced by socially interactive chickadees were not more similar to wild, normal calls. The evidence that some call notes become more "normal" as social interaction increases implies that direct imitation of an external construct does play a role in call learning. Alternatively, the evidence that certain notes do not become more "normal" as social interaction increases implies that direct imitation is not playing a role in all parts of the call. Rather, these notes may be refined on an individual basis, and may make the calls of each individual unique. This chick-a-

dee study highlights the potential for learning mechanisms that are not direct imitation. Tree swallows, which are similar to chickadees in terms of being socially active with a tendency to breed solitarily, may depend on such alternative learning strategies to facilitate the recognition mechanism. Because this study focused on identifying call similarities, the study design is unable to capture those strategies in the results.

5.5 Assumptions

The results and discussion of this study are based on crucial assumptions, and these should be considered when evaluating the validity of this study. The assumptions described in this section are concerned with the inherent nature of nestling begging calls and parent contact calls, and the implications of those characteristics in the proposed recognition mechanism. The assumptions here apply to both parent and nestling calls, to just nestling calls or to just parent calls.

One of the most fundamental assumptions being made is that the call parameters that were measured – duration, frequency modulation, entropy and mean frequency – capture the individuality or similarity of contact or begging calls. Some of these parameters may be poor predictors of those factors, and there may be other call parameters that have not been considered which could explain the variation. Furthermore, similar experimental or cross-fostering studies that aim to describe the effect of genetics and environment on nestling call structure have found that certain combinations of weighted parameters are able to explain variation in call similarity and individuality (Hughes, Nowicki&Lohr 1998, Jacot&Reers 2010). Therefore, an alternative statistical method that is able to simultaneous weigh and group multiple parameters, such as the

discriminant function analysis used by Hughes, Nowicki&Lohr (1998) and Jacot&Reers (2010), may have yielded more significant results in this study.

An important assumption made about the nestling begging call is that it is somehow related to the parent contact call, for example as a precursor. Very little is known about vocal development after fledging, which is when nestlings develop all of their adult calls (Roberston et al. 1992). This assumption implies that the begging call is composed of acoustic components that could reflect the specific characteristics of the contact call, thus allowing us to detect call similarity. If this assumption is incorrect, then the reason why we did not detect call similarity could simply be because the begging call does not have a structure capable of reflecting components of the parent call.

Finally, two important assumptions were made about the adult contact calls we collected. First, there were very few parent calls collected per parent, however we are assuming that the mean parent values we used to compare to the nest means are the true means. In reality, we may not have collected enough parent calls to calculate the true means. Second, we have assumed that the parent calls we did record capture the calls that nestlings respond to. We observed visually using Audacity software that parents did not always give similar calls when communicating with nestlings (figure 7). If we had collected more calls, we may have been able to capture more of the variation in the contact calls, and determine if parents have a consistent contact call when communicating with nestlings.
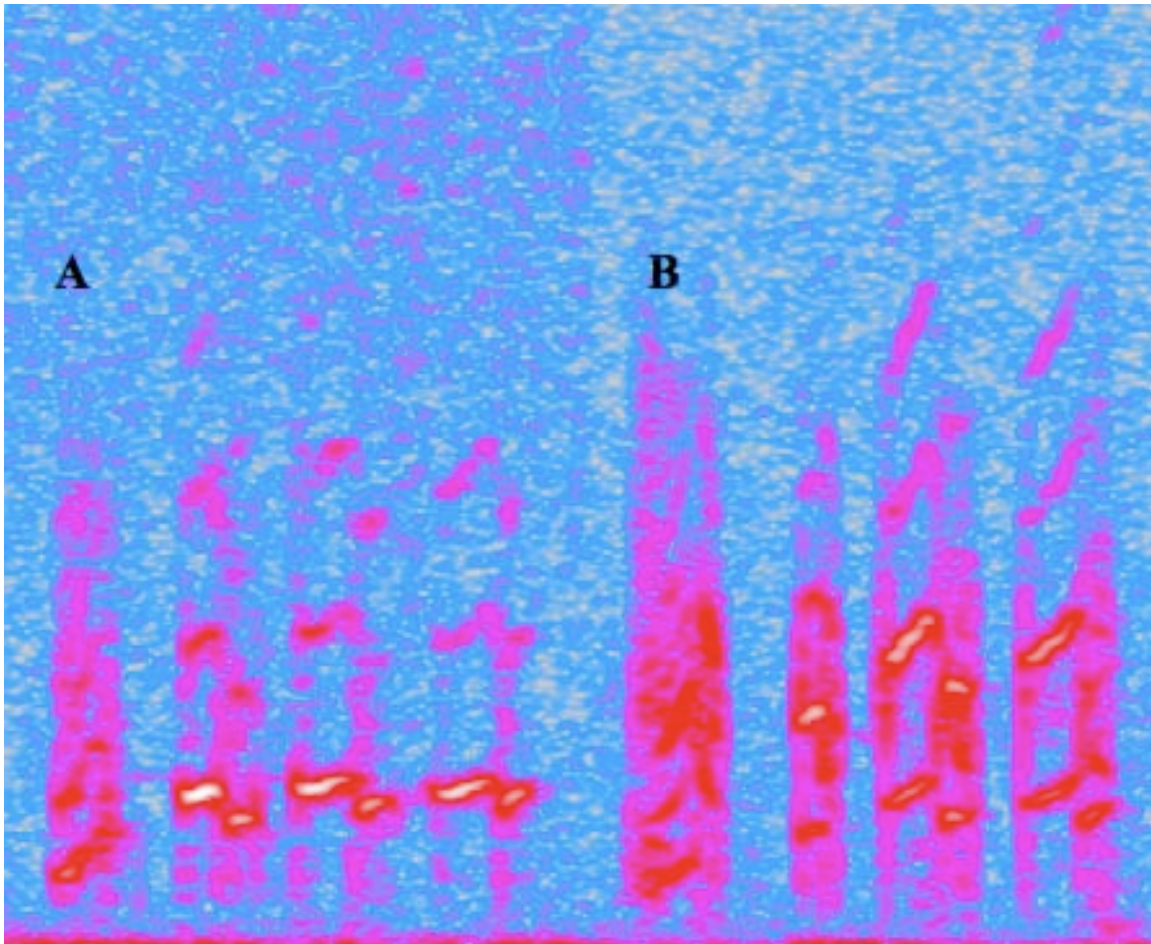
Figure 7. Two calls (A and B) given by the same female parent. Frequency (Hz) is on the vertical axis and time (ms) is on the horizontal axis. The loudest parts of the call are in yellow, the quietest parts are in pink and the background noise is in blue. Note thatboth calls have four syllables, however theydiffer in terms of the dominant frequencies, the duration of certain syllables, and the overall structure of certain syllables.

6.0 Conclusions

The call parameter values of duration, frequency modulation, entropy and mean frequency were not significantly correlated between tree swallow nestling begging calls and parent contact calls. There was also no significant difference in the parent-nestling correlations of male and female parents, nor was there in the parent-nestling correlations of cross-fostered rearing nests, original nests and control nests. These results suggest that,

based on the assumptions outlined in section 5.5, there is little significant call similarity between parents and pre-fledging nestlings, either derived from learning mechanism or a genetically inherited phenotype.

In the context of parent-offspring recognition, the results provide little evidence for a mechanism that allows parents and nestlings to recognize each other through a common cue that they share. However, it may be that the mechanism in tree swallows allows nestlings to recognize parents but not parents to recognize nestlings. In such a mechanism, the individual distinctiveness of the adult call plays a key role, rather than call similarity between parents and nestlings, because the more distinctive the adult call, the easier it is for nestlings to recognize their parents.

Because this study is based on several key assumptions, I recommend that future research on this subject address those assumptions first. Specifically, future research could focus on post-fledging vocal development and variation in the contact call structureof distinct tree swallow adults. Finally, further investigation should explore the ontogeny of vocal individuality in tree swallows, and the role that vocal individuality may play in the tree swallow parent-offspring recognition mechanism.

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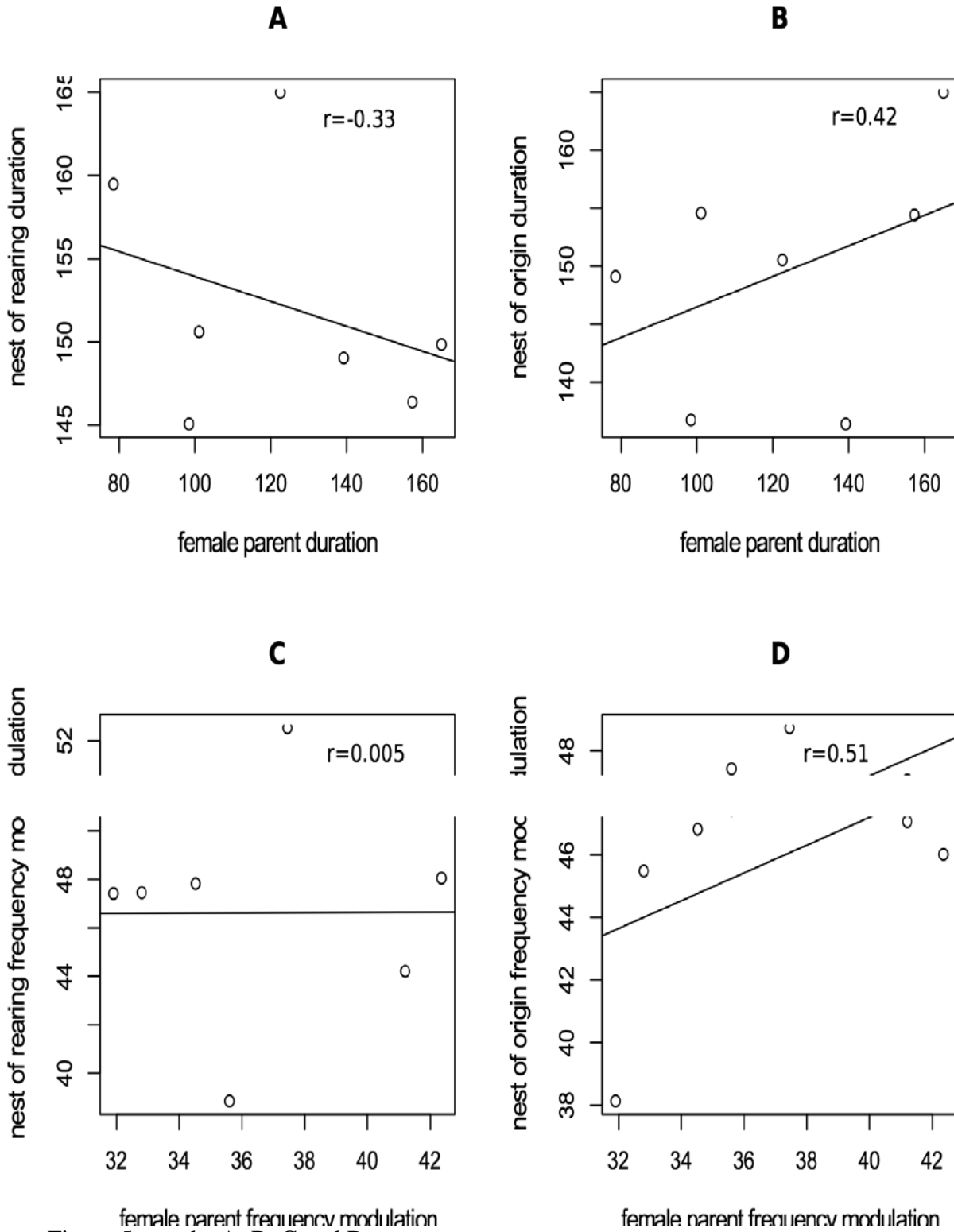
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Acknowledgements

APPENDIX A – Figure 4 A-B

Figure 5, graphs A, B, C and D.

APPENDIX A – Figure 4 E-H

Figure 5, graphs E, F, G and H.

APPENDIX A – Figure 4 I-L

I

r=-0.79

nest of rearing duration / male parent duration

J

r=-0.15

nest of origin duration / male parent duration

K

r=0.82*

nest of rearing frequency modulation / male parent frequency modulation

L

r=0.67

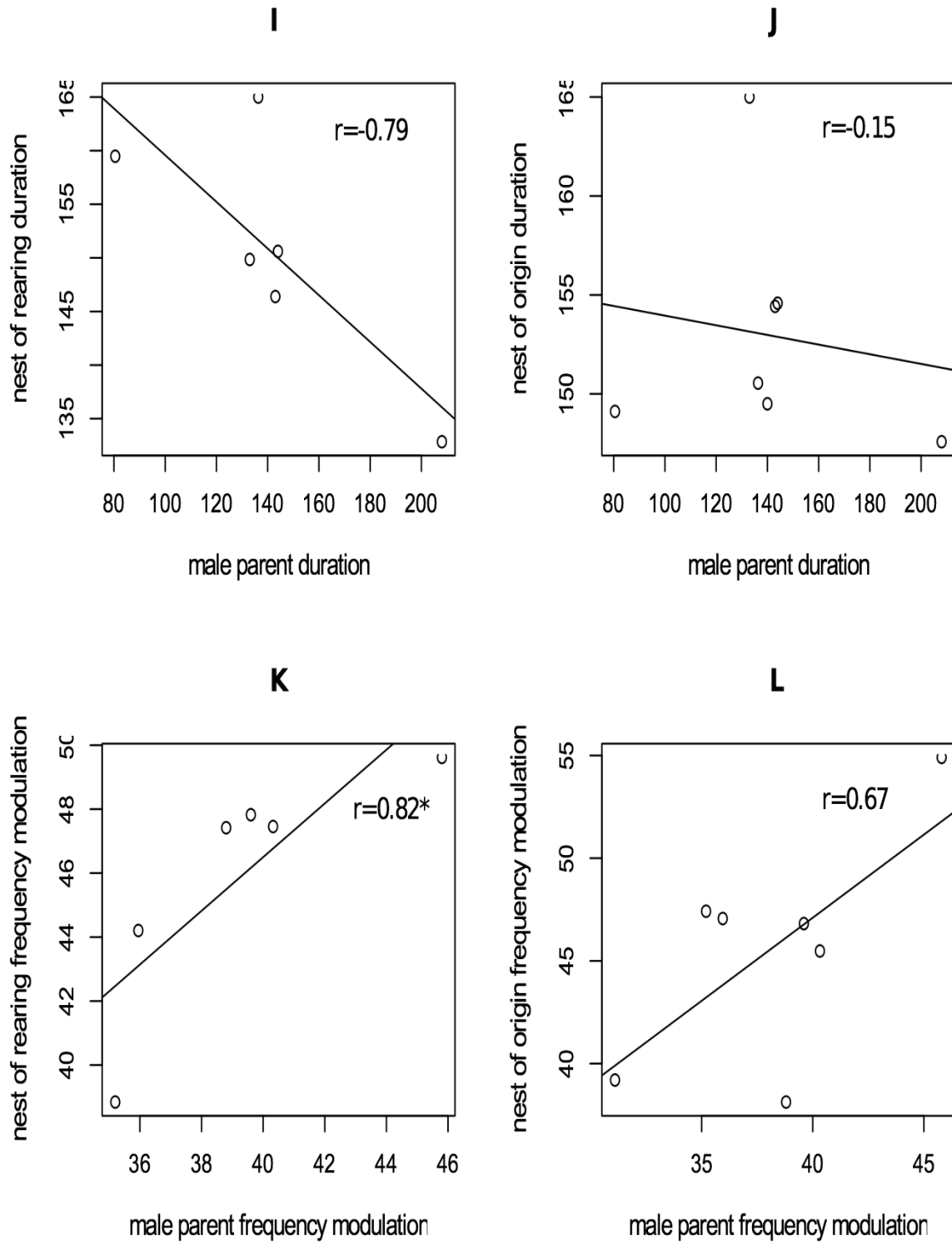nest of origin frequency modulation / male parent frequency modulation
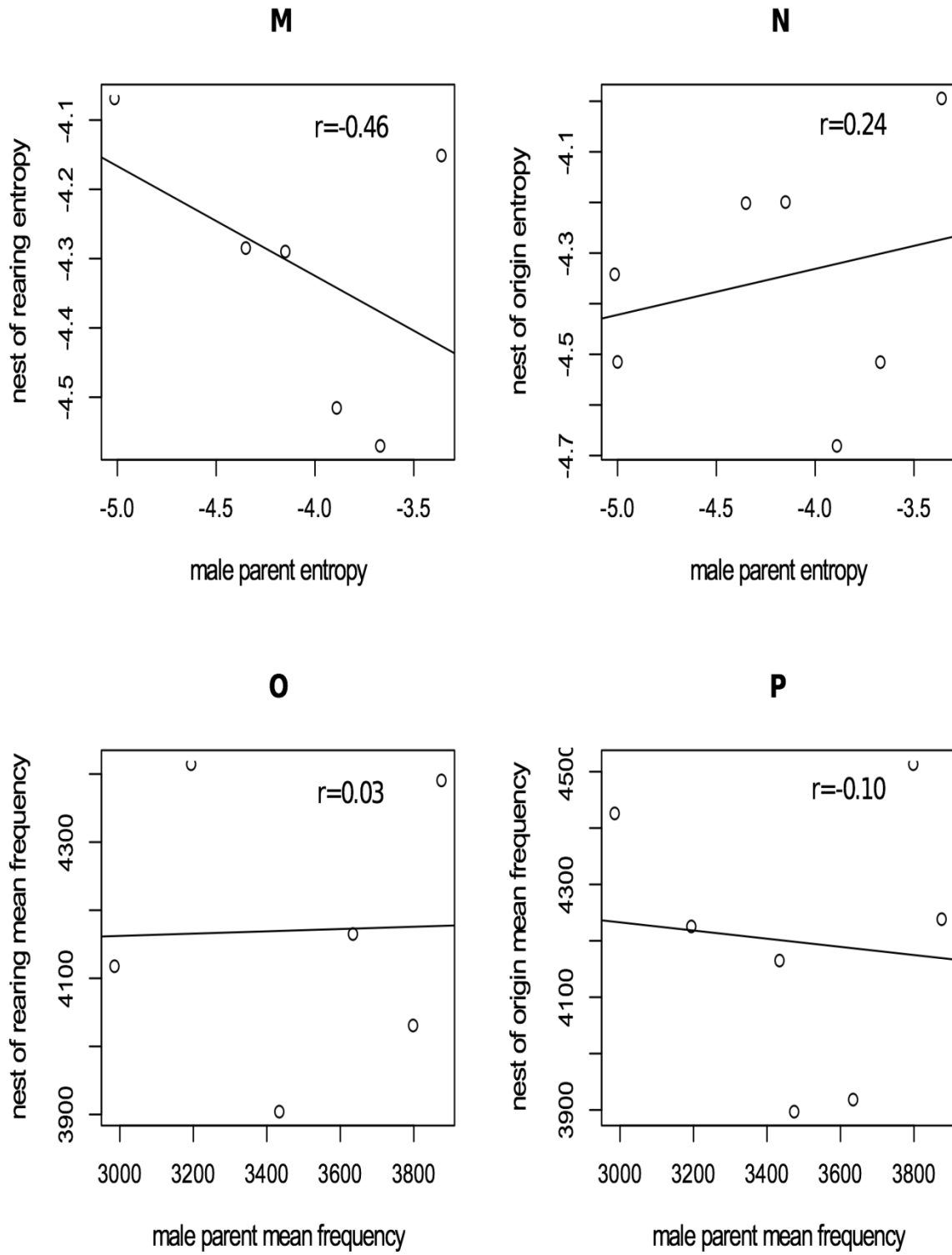
Figure 5, graphs I, J, K and L.

APPENDIX A – Figure 4 M-P

Figure 5, graphs M, N, O and P.