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The development of begging calls in Yellow Warblers

An Honors Paper for the Department of Biology

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Abstract

Nestling birds use begging calls to solicit resources from adults. Efficient transmission of calls is necessary for motivating parental feeding and outcompeting siblings. However, ambient acoustic masking and costs such as predation may influence the structure of the calls. While many interspecific comparisons of begging behavior have been made, the ontogeny of calls is understudied. In this study, Yellow Warbler (*Setophaga petechia*) begging calls were recorded and analyzed at different stages of nestling development to document changes in acoustic structure and gain insight into the selective forces that influence call development. Begging calls increased in peak frequency, frequency range, and amplitude during the 5-day recording period. Call duration did not change with age. Call structure did not differ between nestlings living in distinct acoustic environments. As begging calls increase in amplitude with age, perhaps due to increased food needs and competition from nestmates, nestlings may compensate for increased predation risk by increasing the peak frequency of the calls. Higher frequency calls attenuate more quickly than do low frequency calls and fall outside the frequency range of maximum hearing sensitivity for some potential predators. Previous studies on warbler begging have shown that nestlings of ground-nesting warblers, which are subject to higher rates of predation, beg at higher frequencies than do nestlings of tree-nesting warblers. This study supports the hypothesis that changes to begging call structure during development mirror the differences in call structure of species under different predation risks.

Introduction

Animals require effective communication to interact successfully with other organisms. For many vertebrates, vocal signals are the most direct and conspicuous forms of communication and convey a diverse range of information (Yahner, 2012). For example, passerine songs carry information about condition and individual identification wheras calls can code information about location and distress (Read & Weary, 1990; Sharp *et al*. 2005; Templeton *et al*. 2005). Evolutionary pressures have molded the structural components of vocalizations to improve their efficacy (Gould & Lewontin, 1979; Endler, 1993). In this study, I investigated the ontogeny of Yellow Warbler (*Setophaga petechia*) nestling begging calls to learn about the selective pressures that may influence their structure.

Nestlings and fledglings use begging calls to solicit food from provisioning adults (Cotton *et al*. 1996). Morphology, parents, siblings, parasites, predators, and environmental factors have all been shown to influence the structure and intensity of begging calls (Briskie 1994; Haskell 1994; Cotton *et al* 1996, McCarty 1996; Leonard & Horn 2006). Selection's influence on ontogeny, however, has remained largely unexplored. I focused on the constraints and pressures that are likely to directly affect the acoustic structure, and particularly the acoustic frequency, of nestling calls during development.

Body size and syrinx development likely impact the frequency range over which nestlings can vocalize. Generally, smaller animals have vocal producing structures (e.g. a bird's syrinx) of smaller mass, which constrains them to vocalize at a higher frequency (Ryan & Brenowitz 1985; Wallschlager 1980; Gerhardt 1994). Morphology further constrains communication because high frequency sounds attenuate more quickly than do low frequency sounds, restricting the distance over which a given organism can signal (Gerhardt 1994). While the implications of these constraints may influence nestling begging, a purely morphological model suggests that nestling growth over time should cause a decline in the fundamental frequency of their begging calls.

While begging call development is likely broadly governed by nestling growth, begging calls are also influenced by other factors, including adult hearing sensitivity, predators, and ambient noise. The most sensitive hearing of adult songbirds usually correlates with the dominant frequency at which they vocalize to allow efficient signal transmission. The hearing of many birds is most sensitive from 2-3 kHz, although many passerines can hear well up to 6 kHz (Henry & Lucas 2010: Gleich *et al*. 2005). Consistent with morphological constraints on vocalization, smaller birds tend to have greater sensitivity to higher frequencies, although the sound transfer efficiency of the columella, the sound transmitting bone in the inner ear of birds, may limit high frequency hearing (Henry & Lucas 2010). In the absence of other selective pressures, begging calls would be expected to fall within the best hearing range of their parents, as this would maximize transmission efficiency. This model predicts nestlings will not change the frequency at which they beg over time, as adult birds have static hearing sensitivity thresholds over the timescale of nestling development.

Begging calls may also be structured to escape the attention of eavesdropping predators. The increased amplitude of the most intense begging calls, given when nestlings are hungriest, has been shown to attract predators (Haff & Magrath 2011). Nestlings can compensate for the increase in amplitude by altering the frequency at which they beg, either to avoid the hearing sensitivity range of the predator or to decrease the distance over which the calls travel. For example, nestlings of ground-nesting warbler species, which are more vulnerable to predation than are tree-nesting species, begged at higher frequencies than did those of tree-nesting species, allowing calls to attenuate more quickly and thus avoid detection by predators (Haskell 1999). A predation model suggests that call acoustic frequency should be positively correlated with predation risk and that call frequencies should avoid the hearing ranges of potential predators

Ambient noise may mask the peak frequency of begging calls, causing nestlings to alter the frequency or increase the source level at which they beg to adults in order to be heard. Anthropogenic ambient noise has altered vocalizations of songbirds and marine mammals (Ryan & Brenowitz 1985; Parks *et al*. 2007). For example, Great Tits (*Parus* major) in urban areas have developed songs with higher minimum frequencies than those of birds singing in forest environments (Slebbekoorn & Peet, 2003). Experimental ambient white noise has also caused Tree Swallow (*Tachycineta bicolor*) nestlings to increase the amplitude, and in some cases the frequency range, of their begging calls, suggesting that the masking effects of anthropogenic ambient noise may act as a selective pressure on begging calls as well (Leonard & Horn 2008). If selective pressures select for efficient begging call transmission, then calls should occur within the quietest frequency ranges of their respective ambient soundscapes. The extent to which begging calls are modified based on ambient noise may provide insight into the plasticity of nestling vocalizations.

Previous studies on begging ontogeny suggest the changes to call structure during development are unique to a given species. Nestling Tree Swallows increased the rate and amplitude of their calls with age, but peak frequency did not change over time (Leonard & Horn 2006). There were no consistent trends in the development of the maximum frequency of ten wood warbler species with age, with some species increasing the maximum frequency of begging calls, some decreasing, and others begging at variable frequencies throughout their nestling period (Haskell, 1999). Phylogeny's limited influence on begging suggests the calls comprise a plastic trait that is adjusted quickly based on environmental pressures.

In this study, I recorded Yellow Warbler nestling begging calls to gain insight into the selective pressures acting most strongly on begging development. Yellow Warblers nest in low shrubs or ferns near the ground and may therefore be vulnerable to both mammalian and avian predation, so their begging calls were expected to be higher in frequency than those of tree-nesting nestlings (Cain *et al.* 2003). Due to morphological constraints of the nestling vocal system and limits on maximum hearing sensitivity of parent birds, begging calls were expected to decrease in frequency with age to maximize signal transmission and communication efficacy. Finally, nestlings in a shore environment, which contains noise from gulls (*Larus* spp.), waves, and wind, were expected to beg more loudly and at higher peak frequencies than nestlings begging in inland environments.

Methods

Study Site

This study was conducted at the Bowdoin Scientific Station on Kent Island, in the Gulf of Maine in New Brunswick, Canada (44˚ 35' N, 66˚ 45' W). On Kent Island, Yellow Warblers defended territories on the forest edge, near white spruce (*Picea* *glauca*) stands, and nested between 0.06 and 37.88 m from the forest edge. Nests were located in gooseberry (*Ribes uva-crispa*) and raspberry (*Rubus* sp.) bushes as well as in beds of mountain and evergreen ferns (*Dryopteris campyloptera*, *D. intermedia*). Five females nested in gooseberry bush that bordered Herring Gull (*Larus argentatus*) nesting colonies on the shore, which numbered between 20 and 60 individuals.

Merlins (*Falco columbarius*) and at least one Peregrine Falcon (*Falco peregrinus*) potentially preyed on adult birds and fledglings. Herring Gulls (*Larus argentatus*), Great Black-backed Gulls (*Larus marinus*), American Crows (*Corvus brachyrhynchos*), and Common Ravens (*Corvus corax*) might have fed opportunistically on eggs, nestlings, or fledglings. There are no mammalian predators on Kent Island.

Nest Site Characterization

Nest sites were characterized by vegetation, proximity to the forest edge, gull density, and ambient noise. Plant species were noted at the nest and in the surrounding area up to the forest edge. The island's forest edge was tracked using a Garmin eTrex GPS (Garmin Ltd., Olathe, KS) and was subsequently mapped in ArcGIS (v. 10.2, Esri, Redlands, CA). Adult gull abundance data were taken within a 100 m radius of each nest using point counts.

Ambient noise was characterized for 5 min per day at each nest site, 3 m away from the nest. Each 5-min recording was preceded by a 5-min buffer period in which the recorder operator was able to travel at least 300 m from the nest site to avoid influencing the environment's soundscape. All nest sites were recorded on the same day, in succession based on proximity. This procedure was repeated on five days. Recording began at a different nest on each day, but the order in which nests were recorded remained the same. Four recording sessions were conducted from 0830 hr to 1300 hr and one was conducted from 1300 hr to 1700 hr. All recordings were taken intrasonically with an SM2 Bat Song Meter (Wildlife Acoustics, Concord, MA) at a sampling rate of 32 kHz with a high pass filter of 1 kHz. The recorder was placed 65 - 70 cm off of the ground.

Ambient soundscape recordings were characterized using a Discrete Fourier Transform (DFT) in the selection spectrum view in Raven Pro (v x.x, Cornell Laboratory of Ornithology, Ithaca, NY) to give an approximation of the differences in amplitude at different frequencies at a given nest site. Soundscape mean amplitude was measured from 1-16 kHz every 0.25 kHz. Most nest sites had two acoustic regions of high-intensity noise (Fig. 1). The first was from approximately 3-5 kHz. In some nest sites, especially those along the shore, this increase in intensity was caused by gull colonies. In more inland sites, the high-intensity region was shifted to slightly higher frequencies and was caused by songs of passerines such as American Redstarts (*Setophaga ruticilla*), Common Yellowthroats (*Geothlypis trichas*), Savannah Sparrows (*Passerculus sandwichensis*), Song Sparrows (*Melospiza melodia*), Winter Wrens (*Troglodytes hiemalis*), and Yellow Warblers. The second region of higher intensity noise occurred from approximately 11-14 kHz. This increase in intensity occurred across all recordings and was probably the result of microphone feedback.

A principle components analysis was conducted in R to determine whether shore nest sites and inland nest sites were acoustically distinct ambient habitats. The first axis of variance of the PCA output revealed that 88% of the variance in nest site soundscapes aligned with habitat type, indicating that the shore and inland ambient soundscapes were distinct (Table 1, Fig. 2).

Yellow Warbler Recordings

Nestlings from 14 nests were recorded between 3 June and 30 June 2014. Begging calls were recorded at each nest when nestlings were 1 day, 3 days, 5 days, and 7 days old, where 1 day old is the day after hatch day. For 1-day-old nestlings, I stood at the nest for 1 min prior to recording to ensure nestlings were not fed, and then held the recorder approximately 3 cm above the nest. Recordings were 45 - 90 sec. The recording procedures for 3-day-old and 5-day-old nestlings were identical, with the exception of a 2-min food deprivation period for 3-day-old nestlings and a 3-minute food deprivation period for 5-day-old nestlings. For 4 nests, begging calls were also recorded in the absence of a human operator to ensure that human presence did not affect begging call structure. These recordings lasted 20 min and were conducted 10 cm horizontally from the nest. Seven-day-old nestlings were recorded for 20 min at 10 cm from the nest without human presence because 7-day-old nestlings would not beg in response to a handheld recorder at the nest. There was no discrimination of individual begging calls. Fledgling begging was recorded opportunistically whenever fledglings from a known nest were heard begging.

Adult male Yellow Warbler songs were recorded at each nest site, both when sung independent of feeding events and while feeding at the nest. Female “chip” calls were recorded when possible. Adult vocalizations were recorded to determine whether nestlings incorporate elements of adult calls or songs into their begging calls.

All recordings were taken intrasonically with an SM2 Bat Song Meter (Wildlife Acoustics, Maynard, MA) at a sampling rate of 32 kHz with a high pass filter of 1 kHz, or with an M-Audio microtrack II recorder and Sennheiser microphone at a sampling rate of 22 kHz and no high pass filter.

Banding

Six-day old nestlings were banded with Canadian Wildlife Service aluminum bands. Tarsus length and nestling mass were also measured using Vernier calipers and an OHAUS LS 200 top loading balance (OHAUS, Parsippany, NJ), respectively.

Demography

A total of 15 nesting females were followed during the study (Fig. 3). Of those, 13 produced clutches in their first nest, 1 renested once after nest predation and laid a clutch in a second nest, 1 renested twice after nest predation and laid a clutch in a third nest, and 1 renested twice after loss of earlier nests but failed to produce a clutch. Five females produced clutches in territories adjacent to the shore, while 9 females produced clutches in inland territories. Shore nests were characterized as nests built on the edge of the island, within 20m of the high tide line. Inland nests were characterized as nests farther than 20 m from the high tide line. A total of 10 females produced clutches of 4 nestlings, while 2 females produced clutches of 5 nestlings. One female laid 4 eggs but reared a clutch of 2 nestlings after 2 nestlings died at 0-days-old and 1 female laid 3 eggs but only reared 2 surviving nestlings. Of the 14 clutches, 10 broods survived to fledging.

Data Analysis

Audio files were input into Raven Pro 1.4, which constructed a spectrogram for analysis. All analysis parameters were left at initial download settings. To quantify begging calls, I used the spectrogram view to measure the duration, frequency range, and maximum frequency (the highest frequency in the call), and used a DFT in the selected spectrogram view to measure peak frequency (the frequency of the call with the most energy) (Fig. 4). Twenty sequential calls were measured for each recording if available. Calls were measured sequentially because individual calls could not be discriminated. If 20 calls were not available, all calls were measured. All statistical analyses were conducted in R 3.1.1 (R Core Team, 2014). Figures were made in R 3.1.1 and Graphpad Prism 6.00.

Results

Begging Call Characterization

Begging calls were variable between nests and over time. The simplest calls were characterized by chevron-shaped notes that rose to a maximum frequency before falling again (Fig. 5A). The waveform of these notes was periodic, indicating that the calls were pure toned (Fig. 5B). Some calls with the simple chevron shape also contained sidebands, or elements of the call with frequencies next to the fundamental frequency. These appeared as though they were calls stacked on top of the lowest, loudest call (Fig. 6A). Calls with sidebands were characterized by a more complex waveform that included the addition of the sideband frequencies and the fundamental frequencies (Fig. 6B). These calls sounded richer than pure-tone calls. Sidebands were distinguished from harmonics because they occurred immediately above the frequency of the fundamental note, as opposed to one harmonic interval above the fundamental frequency of the call. Sidebands were seen in begging calls throughout development and their prevalence was not related to age (Fig. 6C, One-way repeated measures ANOVA, $p = 0.15$). Nestlings also introduced complexity into their calls in the form of complex modulation, which I defined as additional structural modification that interrupted the smooth curve of the basic chevron shape (Fig. 7A). The prevalence of complex modulation increased significantly with age. (Fig. 7B, One-way repeated measures ANOVA, $p = 0.03$) In some cases, 7-day-old nestling begging calls contained both complex modulation and sidebands (Fig. 7C).

Begging call development

Begging calls given by 1-day-old nestlings were not audible and did not appear on Raven Pro spectrograms. The peak frequency, or the frequency at which the call is loudest, of begging calls increased with age (Fig. 8, Table 2). Likewise, the maximum frequency, or the highest frequency of the call, and frequency range of begging calls increased with age (Table 2). However, no characteristics changed between the begging calls of 3-day-old and 5-day-old nestlings. The duration of begging calls did not change over time, however (Fig. 9, Table 2; Figure 10, Table 2). The amplitude of 5-day-old nestling begging calls was greater than those of 3-day-old nestlings (Fig. 11, Table 4). Peak frequency was not correlated with mass (Fig. 12, $R^2 = 0.06$, $p = 0.49$).

The effect of ambient noise on begging calls

Shore and inland habitats were shown to be distinct using a PCA analysis of habitat spectrogram DFTs (Fig. 2. Although *a priori* discrimination was made between shore and inland nest sites, the PCA results justified treating the two groups as statistically distinct. There were no significant differences in amplitude or peak frequency between calls from the two habitat types at any age (Table 5). All calls were then grouped together to investigate the relationship between island ambient noise and begging calls. As age increased, the range of mean peak frequencies among all nests shifted toward the acoustic "trough" in the soundscape, between the two peaks of increased sound intensity (Fig. 13). The average peak frequency of all begging calls (8.45 kHz) from 7-day-old nestlings aligned with the frequency (8.54 kHz) with the minimum intensity in the acoustic trough (Fig. 13).

Discussion

The peak frequency, frequency range, and amplitude of Yellow Warbler nestling begging calls increased with age. The increase in frequency range and amplitude did not contradict expectations based on morphological constraints. While the peak frequency and structure of calls may vary among nestlings, the development of the syrinx is likely accompanied by increased vocal capability, which may cause nestlings to beg over a greater frequency range. Likewise, begging call amplitude has been shown to increase in Tree Swallows and several species of warblers (Haskell, 1999; Leonard & Horn, 2006). Increased amplitude over time is probably a consequence of larger body size and syrinx development. The duration of calls did not change with age. Nestlings were thus able to vocalize over a greater frequency range without changing the call duration as they aged, indicating a change in vocal capabilities during nestling development.

The increase in peak frequency was not consistent with expectations. Nestlings were expected to decrease the peak frequency at which they begged, both because body size is generally inversely correlated with vocalization frequency in animals and because nestlings were expected to vocalize within the most sensitive range of adult hearing

(Gerhardt, 1994). While the precise hearing sensitivity threshold for adult Yellow Warblers is unknown, they probably hear best over a range from approximately 1 - 5.5 kHz, as this range is consistent across other passerine species including Carolina Chickadee (*Poecile carolinensis*), White-breasted Nuthatch (*Sitta carolinensis*), Tufted Titmouse (*Baeolophus bicolor*), and Song Sparrow (*Melospiza melodia*), and mirrors the typical peak frequency of adult vocalizations (Henry & Lucas, 2010). It is thus likely that an alternative selective pressure caused the increase in peak frequency over time.

The risk of predation may have driven begging calls to increase in frequency with age, because increased call amplitude may heighten predation risk. Begging calls have been shown to attract predators, particularly when nestlings are hungriest and thus beg with the greatest intensity (Briskie 1999; Haff & Magrath 2011). On Kent Island, potential nest predators included American Crows, Herring Gulls, and Great Black-backed Gulls. Hooded Crows (*Corvus cornix*) have excellent hearing between 0.7 kHz and 2.8 kHz and can hear well up 5.6 kHz (Jensen & Klokker 2006). Ring-billed Gulls (*Larus delawarensis*) have been documented to hear best over a range of 0.8 – 3 kHz, and the frequency range of maximum hearing sensitivity is inversely correlated with mass in most species of birds (Thiessen, 1958; Gleich *et al*. 2005). These data suggest that Kent Island nest predators would be unlikely to hear 7-day-old nestling calls except at close proximity, because calls averaged 8.45 kHz among all nests. Begging at high frequencies may reduce the risk of nest predation on Kent Island, but such a strategy may not be as effective in mainland environments. Yellow Warblers nest low to the ground and nestlings may be subject to predation from mammals, such as eastern chipmunks (*Tamias striatus*) (Haskell, 1999). Chipmunks hear well from 0.25 kHz to 45 kHz, suggesting that nestlings would not be able to tailor their calls to avoid mammalian detection (Heffner *et al*. 2001). It is still possible, however, that Yellow Warbler nestlings have evolved begging calls to diminish avian nest predator detection.

Another explanation for the rise in begging call peak frequency is that higher frequency calls would attenuate more quickly than low frequency calls and be less detectable to all potential predators (Haskell, 1999). Among nine families of birds (Picidae, Tyrannidae, Vireonidae, Muscicapidae, Sittidae, Certhiidae, Paridae, Fringillidae, and Parulidae), call frequency was positively correlated with predation risk (Haskell, 1999, Briskie *et al*. 1999). If increasing the frequency of begging calls is a response to increased predation risk across species, then it may function as a strategy to reduce predation risk during nestling development as well. Increasing the frequency of calls could mitigate the predation risk incurred by simultaneously increasing the amplitude of calls, and is a strategy that does not discriminate among predators. This study does not provide experimental evidence to support this hypothesis.

The presence of sidebands in the calls may conflict with this predation pressure model, because sidebands make calls more broadband and might therefore make them easier to locate (Marler, 1955). Passerine alarm calls follow a similar logic. Some species, such as the Black-capped Chickadee, have two types of alarm calls that carry distinct information about predator size, behavior, and threat (Templeton *et al*., 2005). The "seet" call is a high frequency, pure toned sound that is difficult to locate and warns of a high-risk predator, while the "chick-a-dee" alarm call is broadband, is given when a large, but less dangerous, predator is present, and encourages mobbing behavior. If the nestlings' call characteristics were purely selected to avoid detection, then one would expect them to be pure toned, high frequency calls. Thus, alternative selective pressures may contribute to molding call structure. In White-browed Scrubwrens (*Sericornis frontalis*), nestling begging calls had sidebands when parents were visiting the nest, but usually lacked them when parents were absent (Haff & Magrath, 2011). If sidebands increase sound locatability, nestlings may incorporate them into their calls to help parents determine which nestlings are begging. In Yellow Warblers, which have high rates of extra pair paternity, this strategy may be especially pertinent, as decreased sibling relatedness would increase sibling competition and the need for differentiation (Briskie *et al*. 1994; Yezerinac & Weatherhead, 1997). Begging amplitude has been shown to be inversely related to sibling relatedness across species, so it is likely that nestlings have evolved structural mechanisms to outcompete, or at least differentiate themselves from, their siblings (Briskie *et al*. 1994).

Sibling competition may also drive the increase in complex modulation of calls with age. Nestlings may use more complex calls to distinguish themselves as they become more vocally capable. Furthermore, in some species, including the Black Redstart (*Phoenicurus ochruros*), parents divide broods and feed nestlings and fledglings selectively by discriminating begging calls (Draganoiu *et al*. 2006). The incorporation of complex structure may help parents differentiate nestlings. Alternatively, the complex structure might incorporate elements of adult song as a precursor to song learning. If this is the case, complex modulation could be sex specific, as only males sing. This hypothesis could not be addressed in this study because nestling sex was unknown.

While the literature supports a predation reduction model to describe the increase in peak frequency over time, it is also possible that transmission efficacy caused the increase in peak frequency of the calls. By 7 days old, the average call frequency lined up almost exactly with the quietest acoustic region of the island soundscape. Nestling signal transmission to parents might be irrelevant because of the close proximity of nestlings and parents during feeding. However, once nestlings fledge, they move away from the nest and parents may use begging calls to locate individuals. If this is the case, then fledgling signal transmission is much more important and fledgling calls should be expected to avoid environmental masking. Initial investigation into this hypothesis is unsupportive. The peak frequency of two bouts of fledgling begging, one from 11-day-old fledglings and one from 13-day-old fledglings, were recorded during the study and averaged 6.22 and 7.05 kHz, respectively. This is lower than the average peak frequency of 7-day-old begging calls (8.45kHz). However, this sample size is not big enough to rule out this hypothesis. Furthermore, the begging calls of fledglings have to transmit farther than those of nestlings because the parents have to first locate the fledglings. Therefore, there may be pressure to drop the acoustic frequency of calls upon fledging.

Begging calls must be a highly plastic trait to fit the hypothesis that nestlings adjust their calls to avoid regions of acoustic intensity. While Tree Swallow nestlings have been shown to adjust their calls in response to experimental ambient noise, neither the amplitude nor the frequency of Yellow Warbler begging calls differed between shore and inland nests (Leonard & Horn, 2008). The most intense frequency regions of the ambient soundscape did not correspond to the peak frequency of nestling begging, so nestlings would not be expected to adjust the frequency at which they beg to avoid site-specific environmental masking. However, the shore soundscapes were, both statistically and empirically, much louder than inland nests due to gull vocalizations. Thus, nestlings should be expected to increase the amplitude of their begging to counteract the noisier shore environment. This may be an indication that Yellow Warbler begging calls are not plastic enough to differ environmentally. However, it could also imply that the environments were not sufficiently different to cause differential masking, or that variation between nests outweighed any habitat specific differences in begging calls.

It is unlikely that other selective pressures cause an increase in begging frequency during development. While sibling relatedness may influence the presence of sidebands by necessitating individual differentiation, it would not cause an overall increase in call frequency, especially because the high frequency calls likely fall outside the most sensitive range of adult hearing. Instead, sibling competition should cause increases in begging intensity (call amplitude and rate) and individuality (Briskie *et al*. 1994). Importantly, while calls of different frequencies and amplitudes were seen within nests, I was unable to discriminate among individuals in this study, so conclusions about the role of sibling competition on call development could not be determined.

The results presented here provide a detailed description of the structural development of Yellow Warbler nestlings begging calls. The structural development, and particularly the increase in peak frequency, also provide insight into the selective pressures that have influenced begging ontogeny. Like any biological trait, begging calls likely evolved under the push and pull of multiple, and potentially opposing, selective forces (Gould & Lewontin 1979). I suggest that the increase in peak frequency indicates that risk of predation has influenced begging ontogeny in Yellow Warblers, while sibling competition may also play a role in call structure. Without experimental testing, it is impossible to rule out ambient noise as a factor influencing call development, but the similarity between calls of the two, quite distinct, habitat types, as well as the apparent decrease in frequency of fledgling calls, suggests that ambient noise, at least on Kent Island, does not affect begging development.

Future work could address several of the hypotheses proposed above. Studies could investigate the relationship between call frequency and incidence of predation when controlling for call amplitude to determine whether high frequency sound attenuation diminishes predation risk on Kent Island. Work could also determine whether there is a relationship between the presence of sidebands and sibling relatedness, which would help elucidate the selective pressures that mold call structure. Because nestling identity and sex were not controlled for in this study, a detailed analysis of nestling sex and individual begging could reveal more about the causes of individual variation in begging calls. Finally, an investigation of fledgling begging on Kent Island would provide data about begging frequency and could more robustly reveal any relationship between begging frequency and island soundscape.

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Table legends

Table 1. Principle component analysis of ambient soundscapes on Kent Island. The PCA aligns data along the axis of highest variance and then performs similar alignments until all the variance is accounted for. In this test, 88% of the variance was accounted for in the first axis.

Table 2. ANOVAs for Yellow Warbler begging call characters comparing change in peak frequency, maximum frequency, range, and duration with respect to age and nest.

Table3. Tukey's multiple comparison post hoc test from comparisons of peak frequency, maximum frequency, frequency range, and call duration over different ages. Stars indicate significance (*: $p<0.05$, **: $p<0.01$, ***, $p<0.001$)

Table 4. Two-tailed paired t-test comparing the amplitude of begging calls produced by three-day-old and five-day-old Yellow Warblers (nest averages).

Table 5. Two-tailed t-tests comparing amplitude and peak frequency of Yellow Warbler begging calls in shore and inland habitat types. Recorder distance to nest for 3-d-old and 5-day-old nestling recordings differed from that of 7-d-old nestling recordings, so 7-d-old amplitude measurements are not comparable to those from earlier ages.

Tables

Table 1.

	PCA1	PCA2	PCA3
Standard deviations	37.04	12.84	2.92
Proportion of variance	0.88	0.11	0.005
Cumulative Proportion	0.88	0.99	0.99

Table 2.

		Sum of Squares	df	Mean Square	F-value	P-value
Peak Frequency	Age	9800000	2	9800000	43.78	<0.0001
	Nest	17000000	5	1500000	6.8	0.0002
	Residuals	3800000	10	220000		
Max. Frequency	Age	13000000	2	6300000	18.54	0.0028
	Nest	5700000	5	1100000	3.37	0.0484
	Residuals	3400000	10	340000		
Range	Age	5700000	2	5700000	14.28	0.0015
	Nest	9000000	5	820000	2.05	0.089
	Residuals	6800000	10	400000		
Duration	Age	0.01	2	0.0069	0.75	0.4
	Nest	0.01	5	0.01	0.72	0.71
	Residuals	0.16	10	0.01		

Table 3.

	3 d-old – 5-d-old	3-d-old – 7-d-old	5-d-old – 7-d-old
Peak Frequency	NS	*	***
Max. Frequency	NS	*	**
Range	NS	*	**
Duration	NS	NS	NS

Table 4.

Age (days)	N	dB (Mean)	SD	t	df	p
3	9	70.17	4.79	4.04	8	0.0037
5	9	75.76	5.86	-	-	-

Table 5.

	Habitat type	N	Mean (dB)	SD	t	df	P-value
3-d-old call amplitude	Shore	4	73.26	4.56	2.42	4.47	0.07
	Inland	7	66.18	3.14	-	-	-
5-d-old call amplitude	Shore	5	78.34	7.13	1.18	4.63	0.29
	Inland	5	73.96	2.01	-	-	-
7-d-old call amplitude	Shore	3	59.9	2.83	0.37	6.29	0.73
	Inland	8	60.94	5.35	-	-	-
3-d -old call peak frequency	Shore	4	7359.89	1009.3	0.77	4.19	0.48
	Inland	7	6872.12	625.32	-	-	-
5-d -old call peak frequency	Shore	5	7587.42	1148.9	0.04	4.85	0.97
	Inland	5	7610.84	375.47	-	-	-
7-d-old call peak frequency	Shore	3	7836.22	622.45	1.77	3.92	0.15
	Inland	8	8774.59	453.32	-	-	-

Figure Legends

Figure 1. Approximate Fast Fourier Transform of all ambient soundscapes measured at all nests in different habitats on Kent Island. Data points are the average amplitude of given frequencies (0-16kHz). Red nest sites were located on the shore, while black nest sites were located inland. Each symbol represents recording of background noise a different nest for a given frequency. Sound pressure level is the deviation in sound pressure from the ambient atmospheric pressure. N = 14 nests.

Figure 2. Scatterplot of the first dimension of a PCA analysis for nest sight ambient soundscapes. Red points indicate nests found on the shore, while blue points indicate nests found inland. N = 14 nests.

Figure 3. Map of Yellow Warbler nest sites on Kent Island. Points that are touching indicate territories in which the female was forced to renest. N = 15 nest sites, however one female did not produce a clutch.

Figure 4. Measurements of Yellow Warbler begging calls. Color denotes the intensity of the sound, with white describing the most intense, or loudest part of the call. Harmonics were not considered in this analysis. For all analyses, frequency referred to acoustic frequency as opposed to the prevalence of recurrence of calls.

Figure 5. Characterization of Yellow Warbler begging call structure. Simple calls were characterized by a pure tone and chevron shape (A) and have a periodic wave form (B).

Figure 6. Characterization of sideband structure in Yellow Warbler begging calls. Sidebands (A) appeared in some calls, resulting in the addition of multiple frequencies and causing a modulated waveform (B). (C) The prevalence of sidebands among all nests did not change with age (One-way repeated measures ANOVA, $p = 0.15$, $N = 6$ broods).

Figure 7. Characterization of complex modulation in Yellow Warbler begging call structure (A). Complex modulation increased in prevalence with nestling age (B) (One-way repeated measures ANOVA, $p = 0.03$, $N = 6$). In some cases, 7-d-old nestling begging calls contained both sidebands and secondary structure (C).

Figure 8. Mean peak frequencies of Yellow Warbler begging calls at different ages. Data were taken from nest averages Peak frequency within nests increased significantly with age (ANOVA, in terms of age and nest, $p < 0.001$). Boxes extend from 25th to 75th percentiles and show mean. Whiskers show maximum and minimum. $N = 6$ broods.

Figure 9. Mean frequency range of Yellow Warbler begging calls at different ages. Data were taken from nest averages. Frequency range within nests increased significantly with age (ANOVA, in terms of age and nest, $p < 0.01$). Boxes extend from 25th to 75th percentiles and show mean. Whiskers show maximum and minimum. $N = 6$ broods.

Figure 10. Mean duration of Yellow Warbler begging calls at different ages. Data were taken from nest averages. Duration did not change with age (ANOVA, in terms of age and nest, $p = 0.3977$). Boxes extend from 25th to 75th percentiles and show mean. Whiskers show maximum and minimum. $N = 6$ broods.

Figure 11. Mean amplitude of three-day-old and five-day-old Yellow Warbler begging calls. Data was taken from nest averages. Amplitude increased significantly with age (Paired t-test, $p > 0.01$). Boxes extend from 25th to 75th percentiles and show mean. Whiskers show maximum and minimum. $N = 9$ broods.

Figure 12. Correlation of nestling mass and peak begging frequency among seven-day-old Yellow Warbler nestlings Peak frequency was not related to mass ($R^2 = 0.06$, $p = 0.49$, $N = 11$ broods).

Figure 13. Range of mean peak frequencies among all Yellow Warbler nests compared to shore habitat and inland habitat soundscapes. Points on the frequency ranges represent the mean peak frequency for all nests on that day. $N = 14$ nest sites.

Figures

Figure 1.

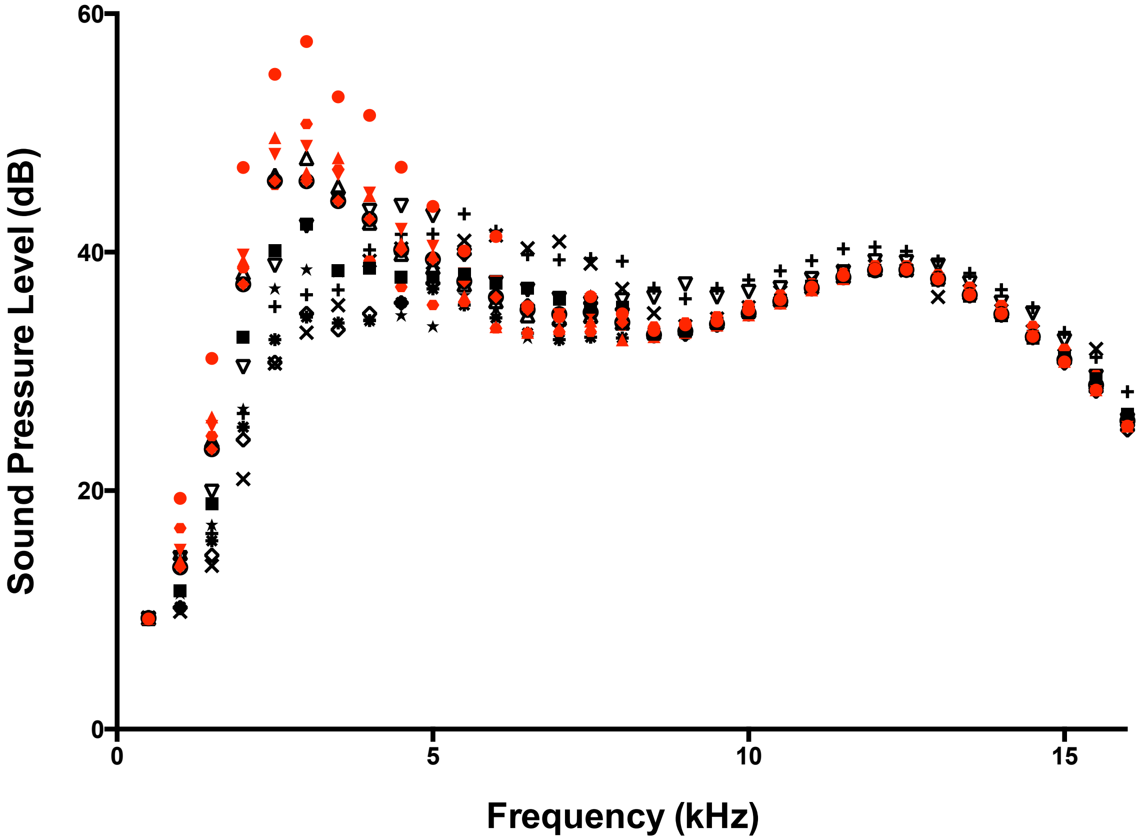


Figure 2.

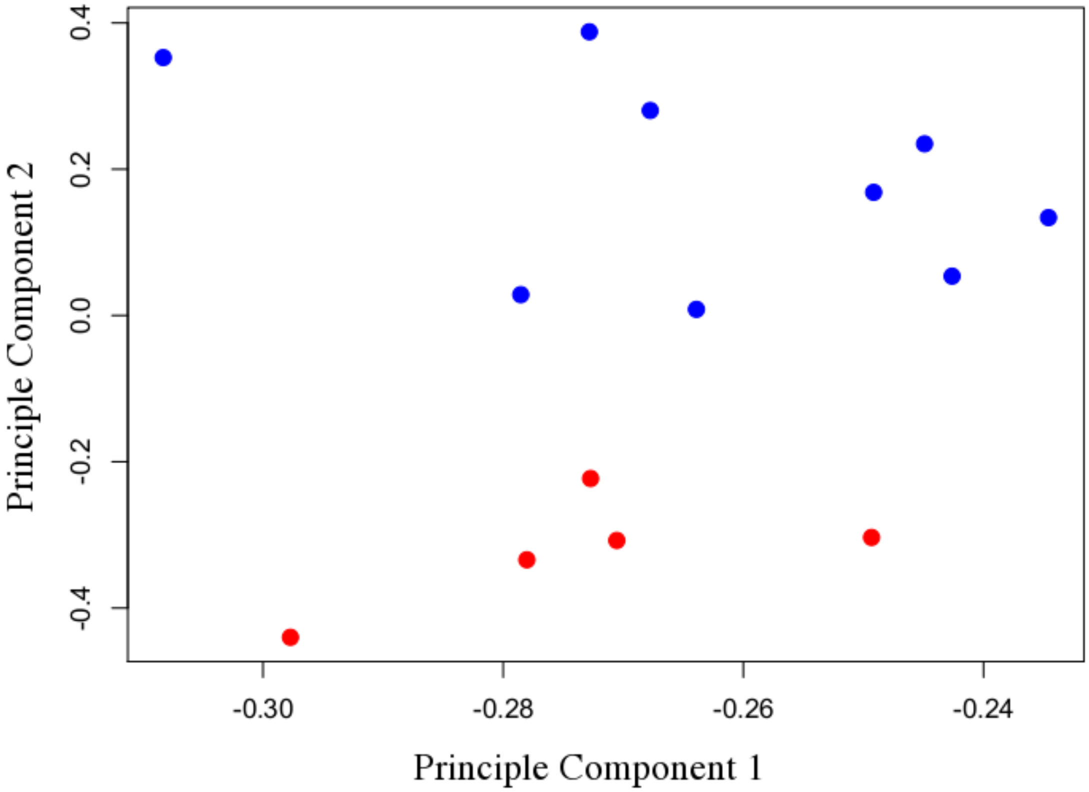

0.4
0.2
0.0
-0.2
-0.4
Principle Component 2
-0.30
-0.28
-0.26
-0.24
Principle Component 1

Figure 3.

Figure 4.

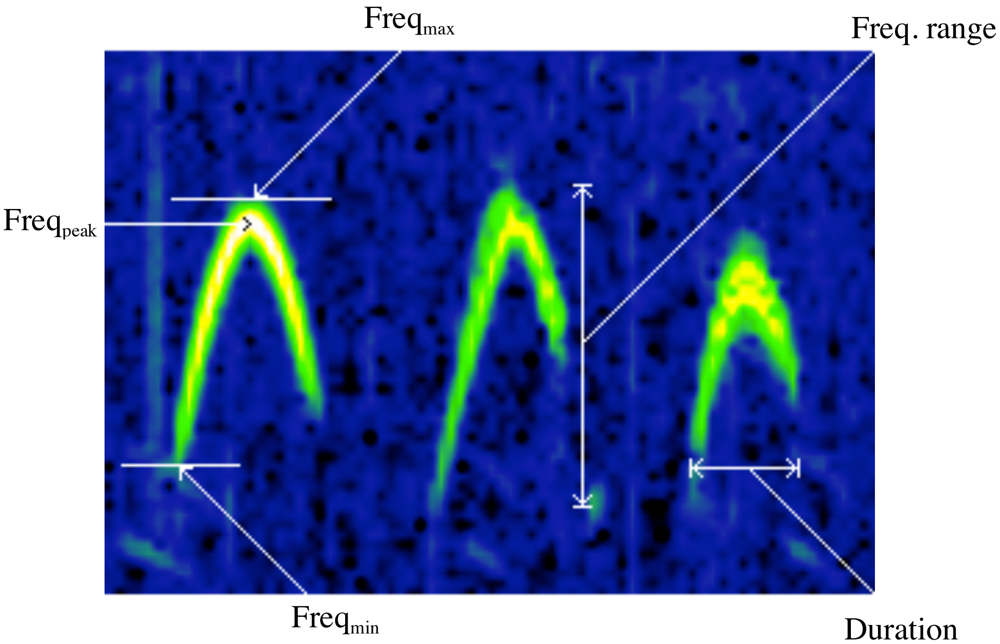
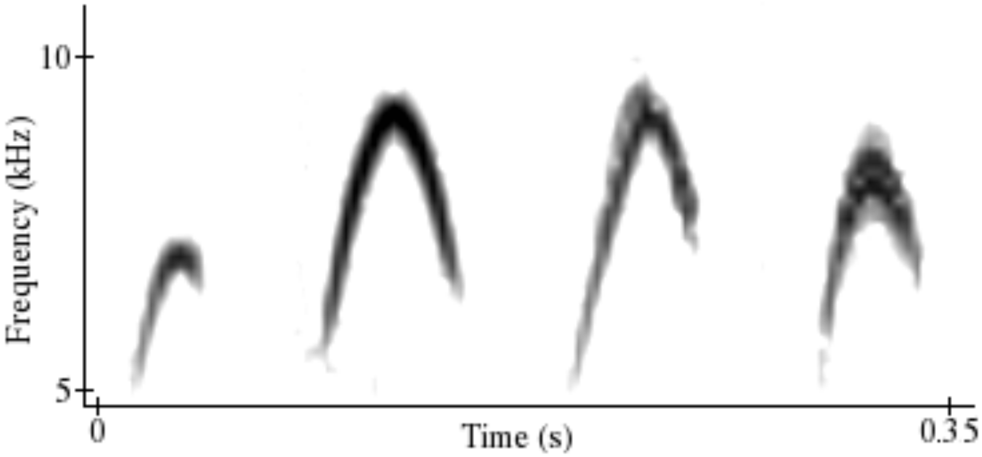


Figure 5.

A.


10
5
Frequency (kHz)
0
Time (s)
0.35

B.

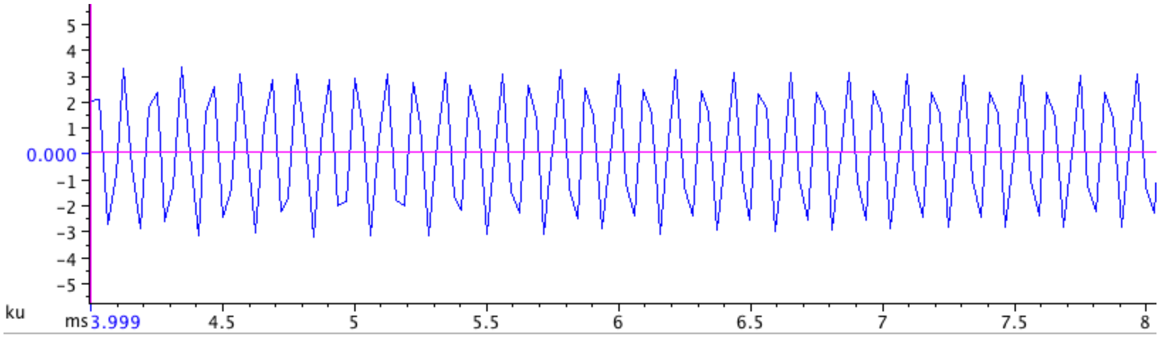
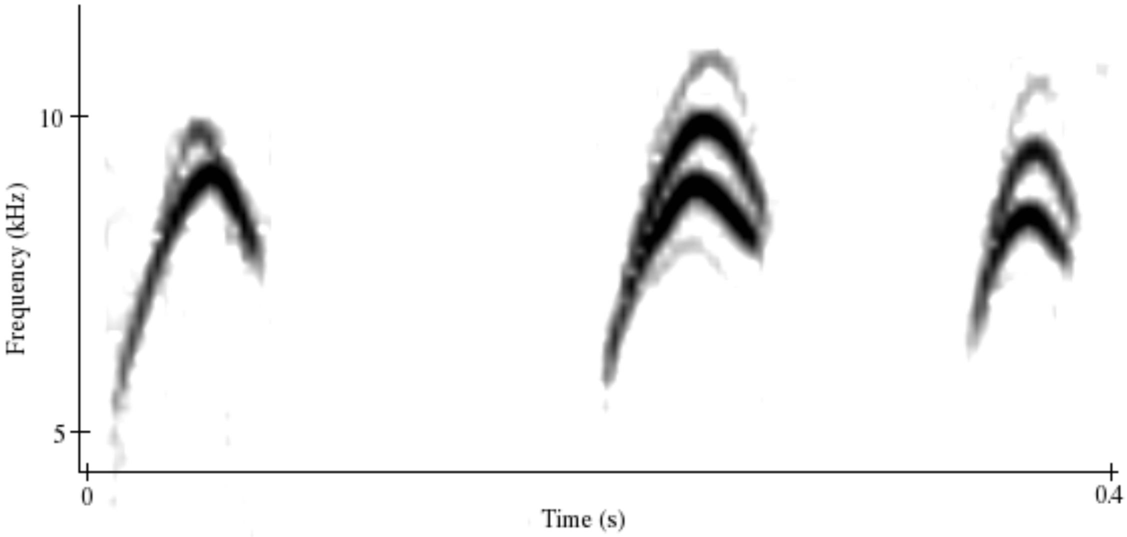

5
4
3
2
1
0.000
-1
-2
-3
-4
-5
ku
ms
3.999
4.5
5
5.5
6
6.5
7
7.5
8

Figure 6.

A.



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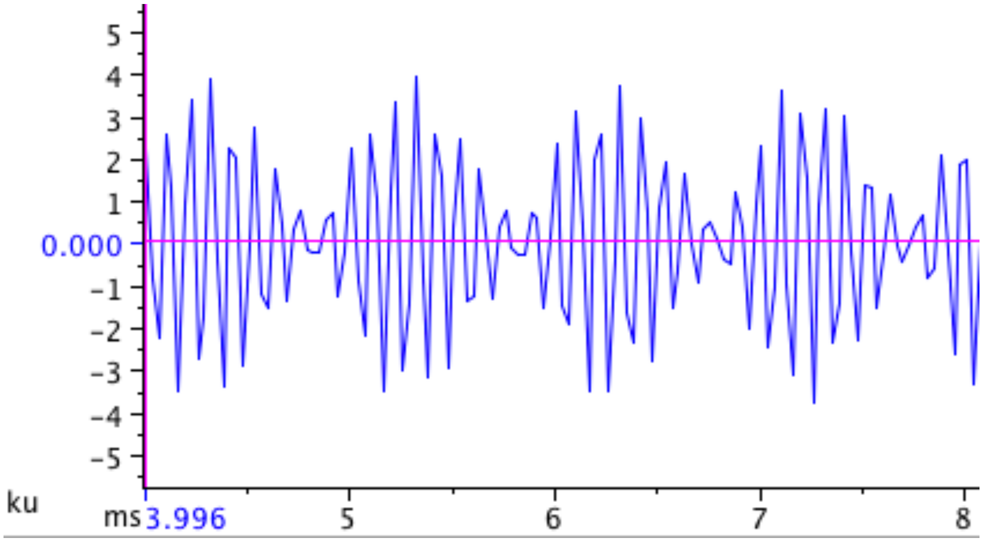


C.

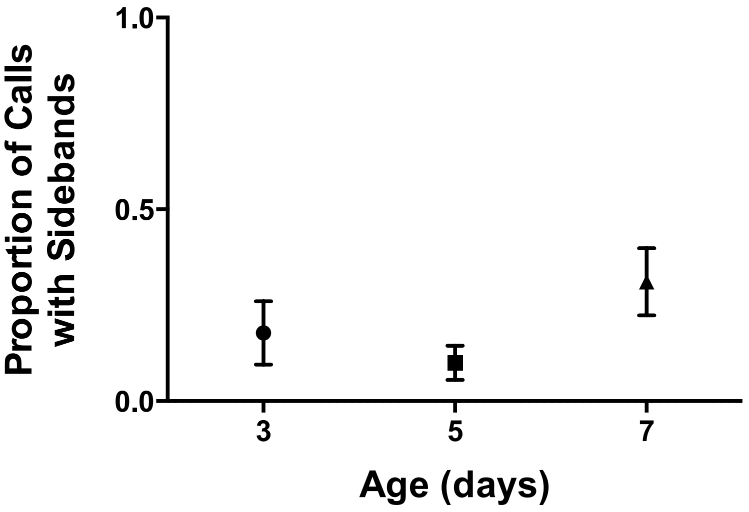
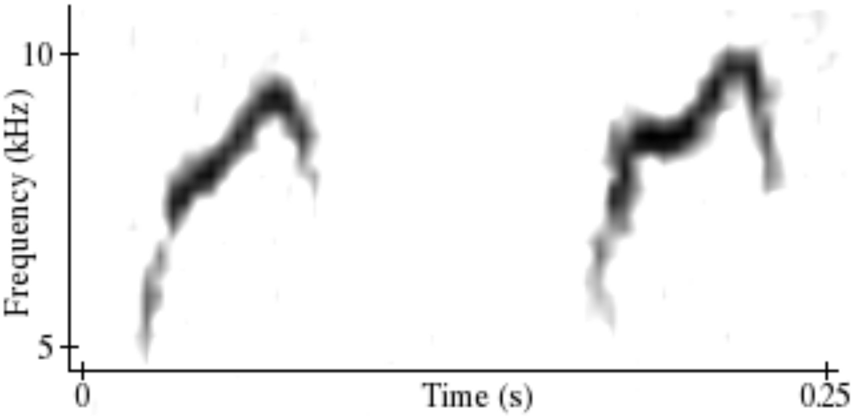


Figure 7.

A.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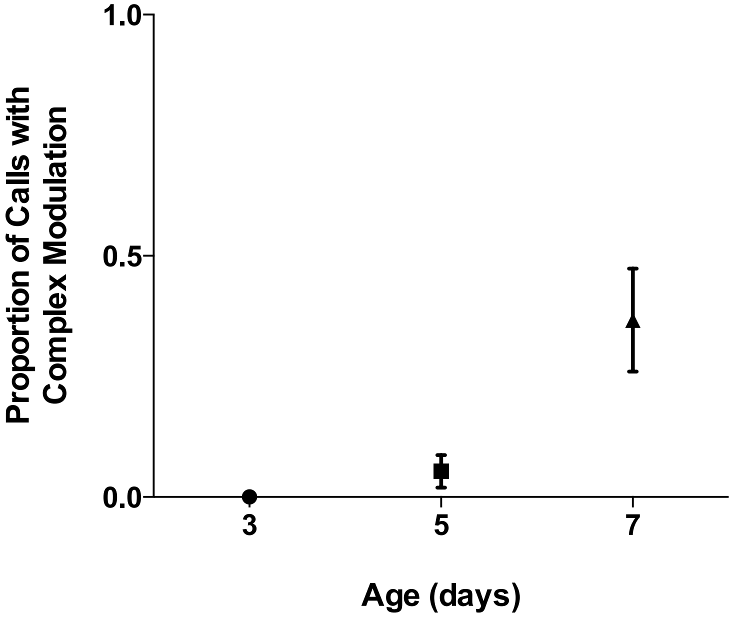
5
Frequency (kHz)
0
Time (s)
0.25

B.


1.0
0.5
0.0
Proportion of Calls with Complex Modulation
3
5
7
Age (days)

C.

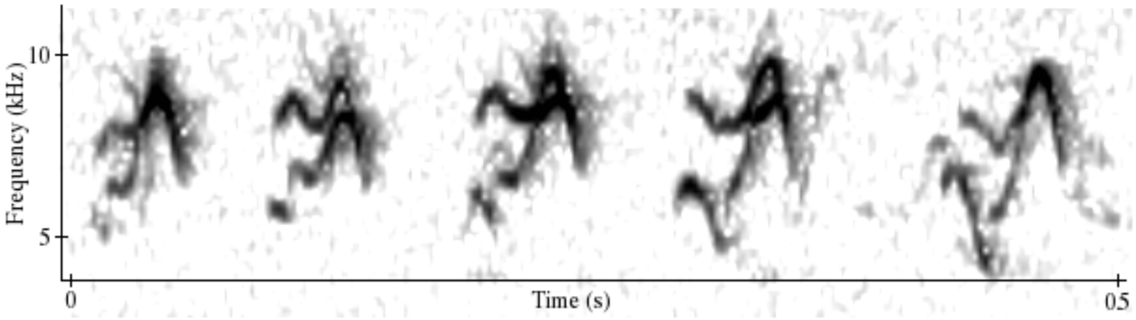
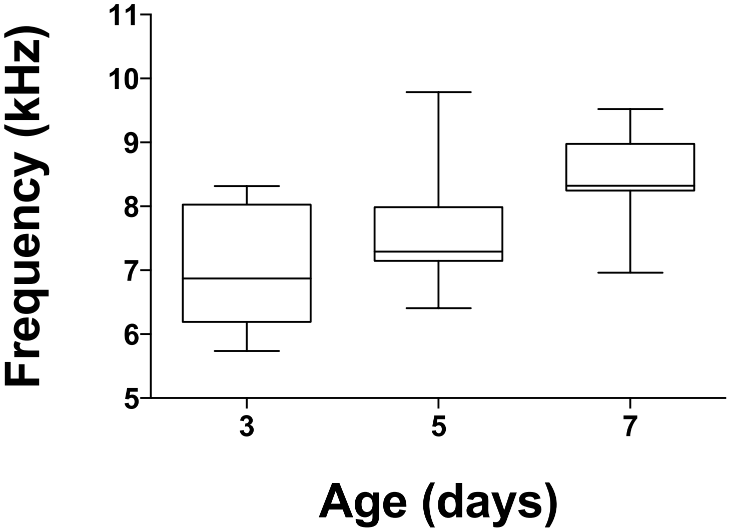


Figure 8.



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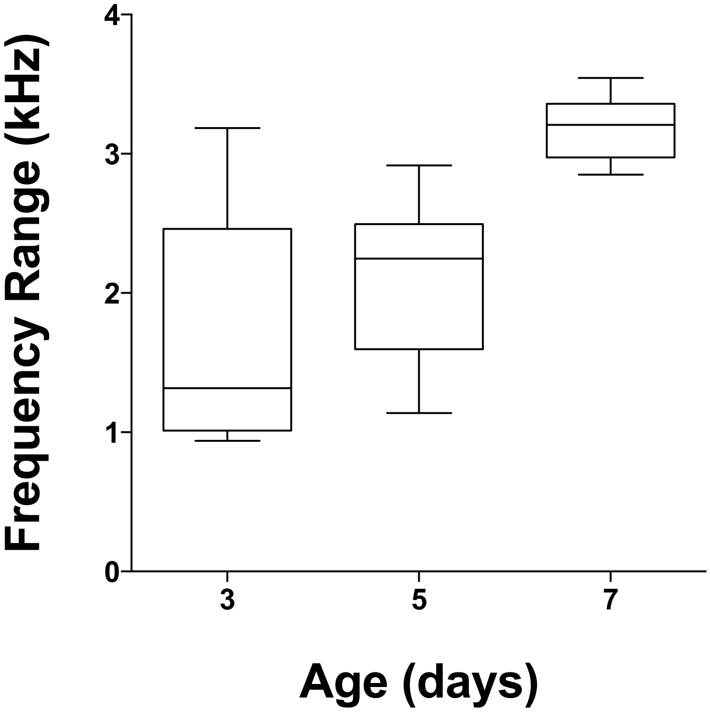
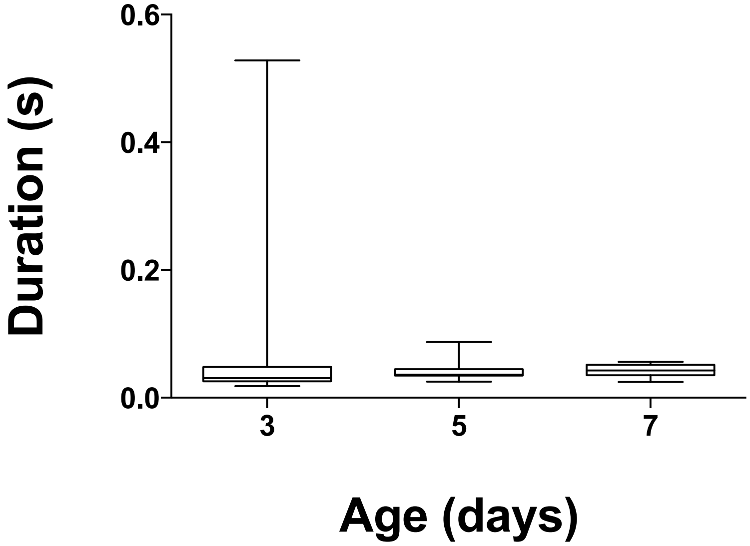


Figure 10.



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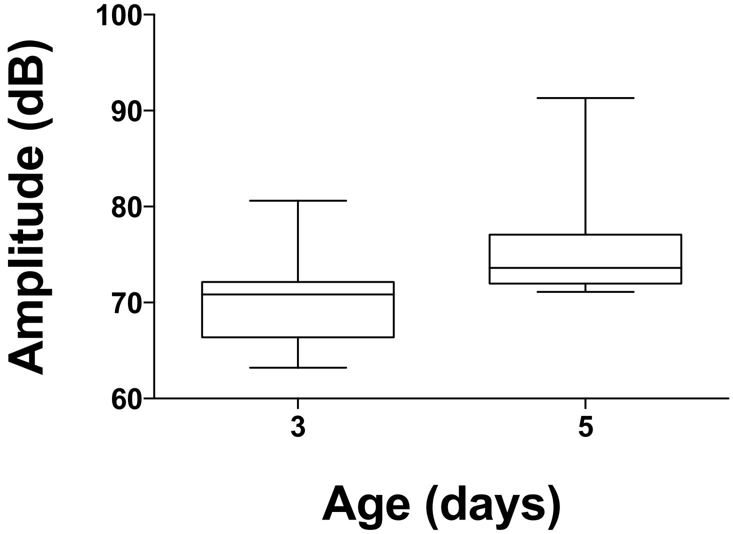

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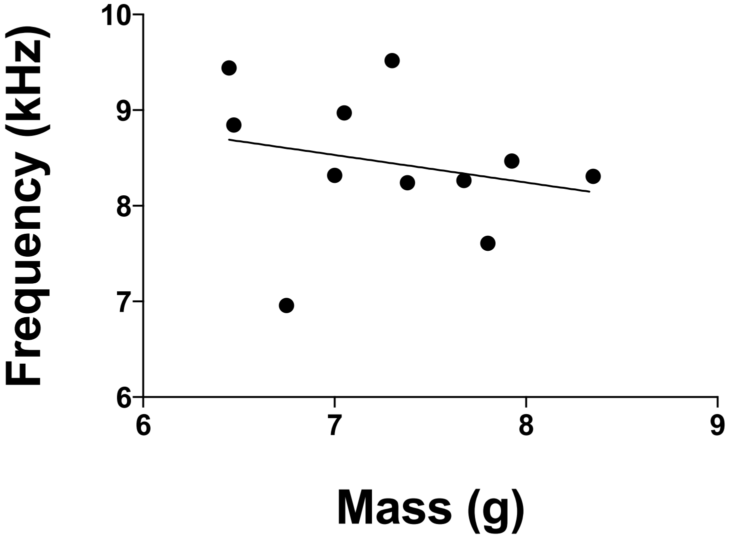
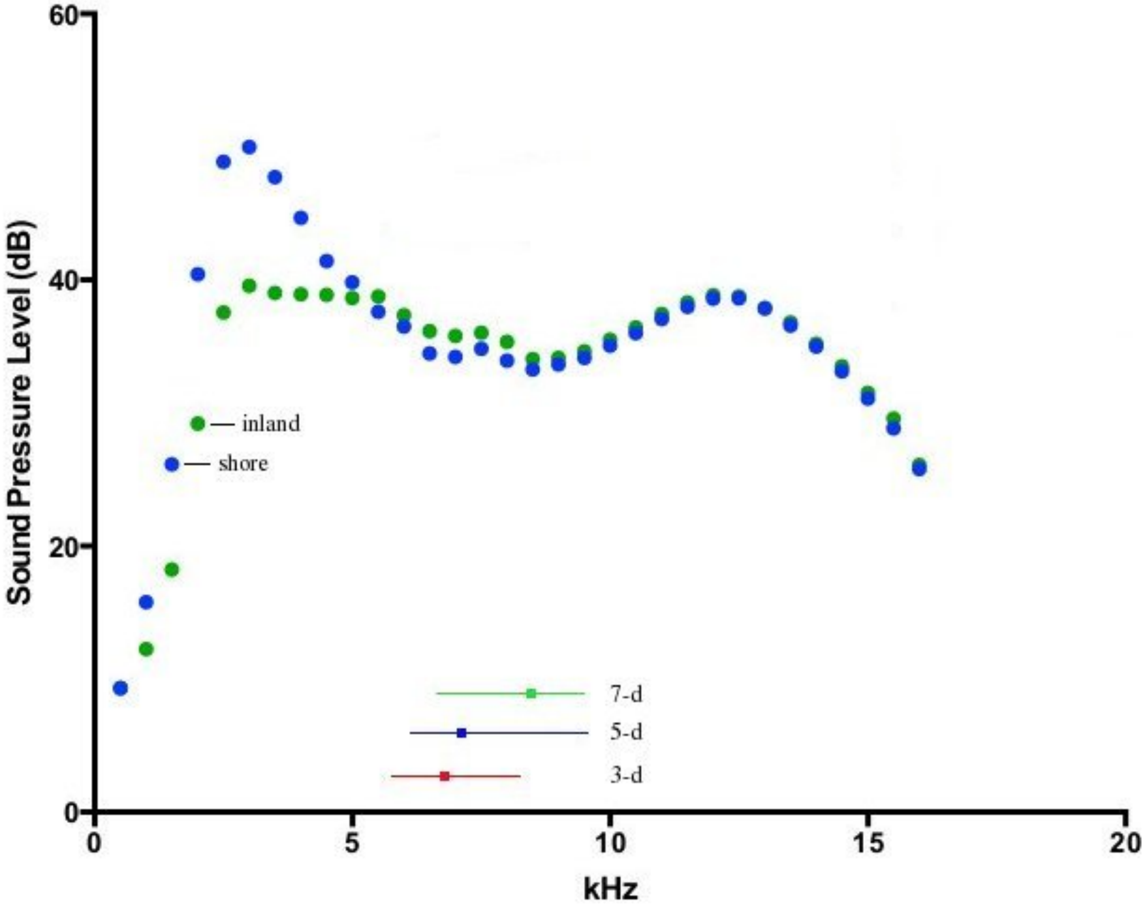


Figure 13.


60
40
20
0
Sound Pressure Level (dB)
● — inland
● — shore
7-d
5-d
3-d
0
5
10
15
20
kHz

Appendix

Nesting Behavior

Yellow warblers tended to choose territories near the forest edge. Nests, including those built by females who renested, averaged 18.3 m ± 16.7 SD (range 0.06 - 64.07 m, *n* = 21) from the forest edge and were found, on average, 0.58 m ± 14.8 SD (range 44 -94, *n* = 18) above the ground. Females built nests in raspberry (*Rubus* spp.) and gooseberry (*Ribes uva-crispa*) bushes as well as amidst wood ferns (*Dryopteris* spp.). Adjacent nests were found on average 102 m ± 21.6 (range 69.8 – 131, *n* = 10) apart, giving an estimate for territory diameter. Nests were constructed from thin grasses and fireweed (*Chamerion angustifolium*) down and were padded with muskrat (*Ondatra zibethicus*) fur, Common Eider (*Somateria mollissima*) feathers, gull (*Larus* sp.) feathers, and trichomes from the stems of cinnamon ferns (*Osmundastrum cinnamomeum*) (Fig. 1). Cup diameter averaged 5.23 cm ± 0.21 SD (range 4.8 – 5.5, *n* =7), although measurements were taken after fledging and could have been influenced by nestling growth and departure from the nest. One nest found on Hay Island appeared to be two- or three-storied but did not contain Brown-headed Cowbird (*Molothrus ater*) eggs. It is possible that the multi-storied nest could have resulted from renesting on top of the original nest after egg predation, rather than from brood parasitism.

Incubation

Only female Yellow Warblers were observed incubating. During incubation events, females shifted position several times but stayed on the nest. At all nests observed, the socially paired male came to feed the female while she was incubating and usually sang before approaching the nest. However, females also rose periodically to forage (Fig. 2). Before returning, many females chipped and were followed to the nest by the male. A 3.2 gram Maxim's IButton (Maxim Integrated, San Jose, CA) was used to record nest temperature every minute during data collection. Female incubation periods ranged from 12 to 15 days from the first egg laid.

Nestlings

Seven of 14 broods had runt nestlings. Nestlings were considered runts if their mass fell below one standard deviation from the brood mean. Eight broods fledged on the 11th day in the nest, while 1 brood fledged on the 10th day in the nest and 1 brood fledged on the 12th day in the nest. Mean nestling brood size, mass, and tarsus length are shown in Table 1.

Fledgling begging and behavior

Fledglings chipped regularly during their first two days out of the nest. Chipping increased in amplitude and was repeated at faster intervals when parents approached with food. During these days, fledglings hid in shrubs, did not fly, and rarely changed location. However, when approached, they hopped between branches or just sat still. During the first two days after fledging, fledglings stayed low to the ground and close to the nest. Four days after fledgling, fledglings were observed away from the nest near the forest edge. When flushed, they were capable of short flights to nearby branches. Once they were near the forest edge, fledglings were quiet unless a parent with food was near. Fifteen days after fledging, fledglings were observed in the canopy of trees and were capable of flight between branches. Fledglings both gleaned insect prey on branches and leaves and were fed by their parents. Yellow first appeared in the plumage on wing primaries and later on the throat and breast.

Adult behavior

Adult behavior was observed throughout the breeding season. The following is an account of behavior as it relates to nestlings and fledglings. Both parents fed nestlings during nestling development. In almost all feeding events, males sang before entering the nest. Both males and females sometimes vocalized directly before feeding, which seemed to initiate nestling begging (Fig. 3). Feeding events were normally spaced by 2-3 min. Often, either the male or female fed nestlings multiple times in a row before the other returned to the nest. Males were observed feeding females several times during the nestling period. In two cases, females were flushed from nests containing 7-day-old nestlings before sunrise, indicating that females brooded during the night.

After fledging, adults appeared to focus on particular fledglings during feeding, bring food to the same fledgling several times in a row. However, it is unknown whether brood division occurred.

Begging call correlation with adult song

The age and timing of vocal learning is diverse among species of songbirds (Brenowitz *et al*. 1997). While the critical song learning periods for many species have been well documented, there is evidence that some birds encode information as nestlings, and even embryonically (Brenowitz and Beecher 2005; Colombelli-Négrel *et al*. 2012). For example, Superb Fairy-Wren (*Malurus cyaneus*) nestlings incorporate elements of female calls given during incubation into their begging calls (Colombelli-Négrel *et al*. 2012). These elements are thought to help females identify brood parasites, such as the Horsfield's Bronze-Cuckoo (*Chalcites basalis*). Black-capped Chickadees have also been shown to begin integrating parts of adult calls into their begging at 8-days-old (Clemmons & Howitz 1990). Furthermore, nestlings begging development has been shown to be similar to song learning physiologically. For example, the variability of male Chipping Sparrow (*Spizella passerina*) begging calls decreased both when nestlings were deafened and when lesions were made in the RA region of the brain (Liu *et al*. 2009). Both experimental procedures have also been shown to reduce song variability and inhibit learning (Liu *et al*. 2009). While selective pressures, such as predation, have caused changes to warbler begging calls, little work has been done to determine whether learning influences call structure. In this study, begging calls of 7-day-old nestlings were compared to the songs of the nestlings' respective social father to determine whether nestlings began incorporating song notes into their calls.

For comparisons, two distinct sample begging calls were taken from recordings of 7-day-old nestlings begging for food. These calls were compared with song recordings of the nestlings' respective social fathers using the Raven Pro 1.4 Correlator tool under manufacturer parameters. The sex of individual nestlings was unknown. Calls and songs were compared from 11 different nests. No correlation was found between any call and its respective song (Figure 4). Correlation values between calls and songs did not exceed 0.06, with 1.00 representing a perfect correlation.

These results indicate that Yellow Warbler nestlings did not incorporate elements of adult song into their begging calls by 7-days-old. One possible explanation is that begging calls may be hardwired in Yellow Warblers. If this is true, then at some point in development juveniles should begin to produce vocalizations that are related to song imitation, rather than food. A second possibility is that begging calls do eventually incorporate elements of adult song, but that this incorporation occurs later in development. Nestling Black-capped chickadees did not start introducing call notes until they were 8-days-old. Therefore, recording calls further into development could determine whether nestling food begging calls transition into song learning.

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Colombelli-Négrel, D., M. E. Hauber, J. Robertson, F. J. Sulloway, H. Hoi, M. Griggio, & S. Kleindorfer. 2012. Embryonic learning of vocal passwords in Superb Fairy-Wrens reveals intruder cuckoo nestlings. Current Biology **22**: 2155-2160.

Liu, W., K. Wada, & F. Nottebohm. 2009. Variable food begging calls are harbingers of vocal learning. PloS ONE **4**: e5929

Table legends

Table 1. Brood size, mass, and tarsus length of 6-d-old Yellow Warbler nestlings on Kent Island.

Tables

Table 1.

Nestlings in Brood	Average Mass	Standard Deviation	Average Tarsus Length	Standard Deviation
4	7.8	0.12	16.35	0.48
5	7.38	0.81	16.28	0.65
4	7.2	0.37	15.65	1.12
4	7.05	0.05	14.975	0.20
4	6.45	0.44	15.775	0.73
5	7.3	0.71	16.42	1.02
4	6.475	1.18	15.325	0.58
4	7.675	0.43	16.2	0.54
4	8.35	0.78	15.775	0.64
2	7	0.6	14.8	0.8
4	7.925	0.44	15.625	0.33
4	8.4	0.29	16.775	0.64
4	7.775	0.08	16	0.19
2	6.75	0.45	14.1	1.4

Figure Legends

Figure 1. Examples of Yellow Warbler nests showing size, materials, and attachment. The nest on the left was a two-story nest but did not contain a cowbird egg. Both the left and middle nest were composed of grass and lined with gull feathers, while the nest on the right was composed of thin plant filament and lined with trichomes from cinnamon ferns.

Figure 2. Ambient temperature subtracted from nest temperature starting at 13:30 during incubation. The rises show brooding events by the female, while the falls show females leaving the nest.

Fig. 3. Example of adult notes prior to nestling begging. These notes, which are dark and occur three times in succession, were often seen just before, or right at the start of, nestling begging calls.

Figure 4. Example of begging call spectrogram correlated with that of an adult song in Raven. The top line in green represents correlation value. The middle region is a spectrogram of the adult song. The lowest region is a spectrogram of a begging call from a 7-day-old nestling. The (mu) units on the correlation are arbitrary units, while (kHz) represents acoustic frequency and (s) represents time.

Figures

Figure 1.

Figure 2.

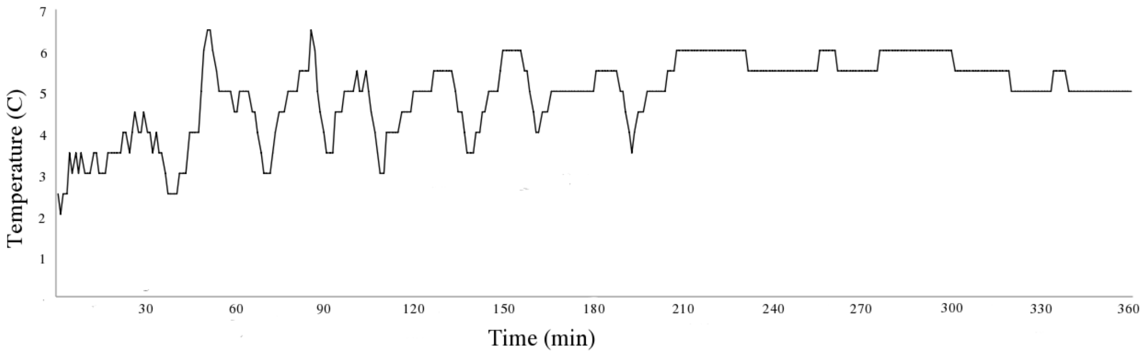


Figure 3.

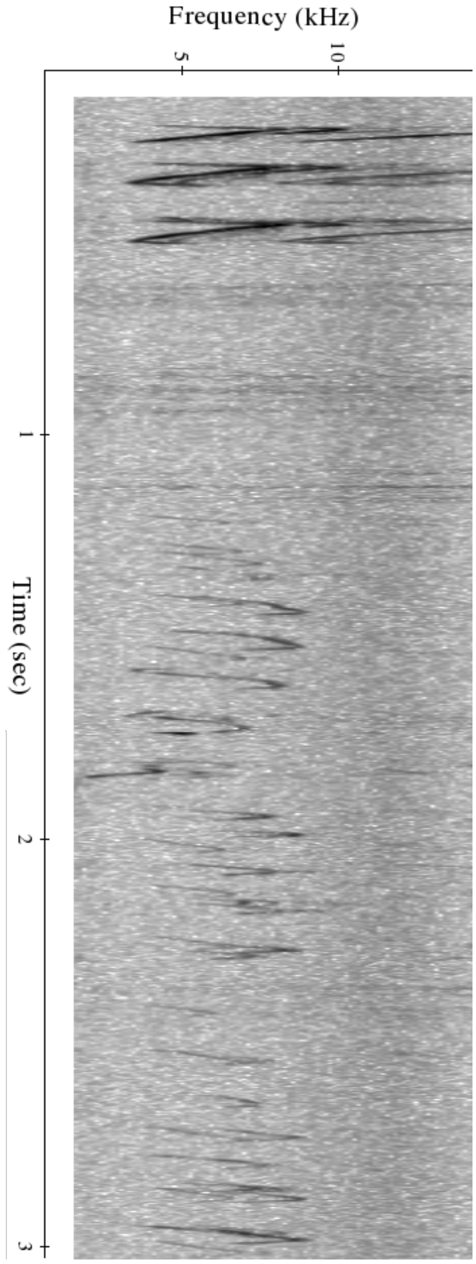
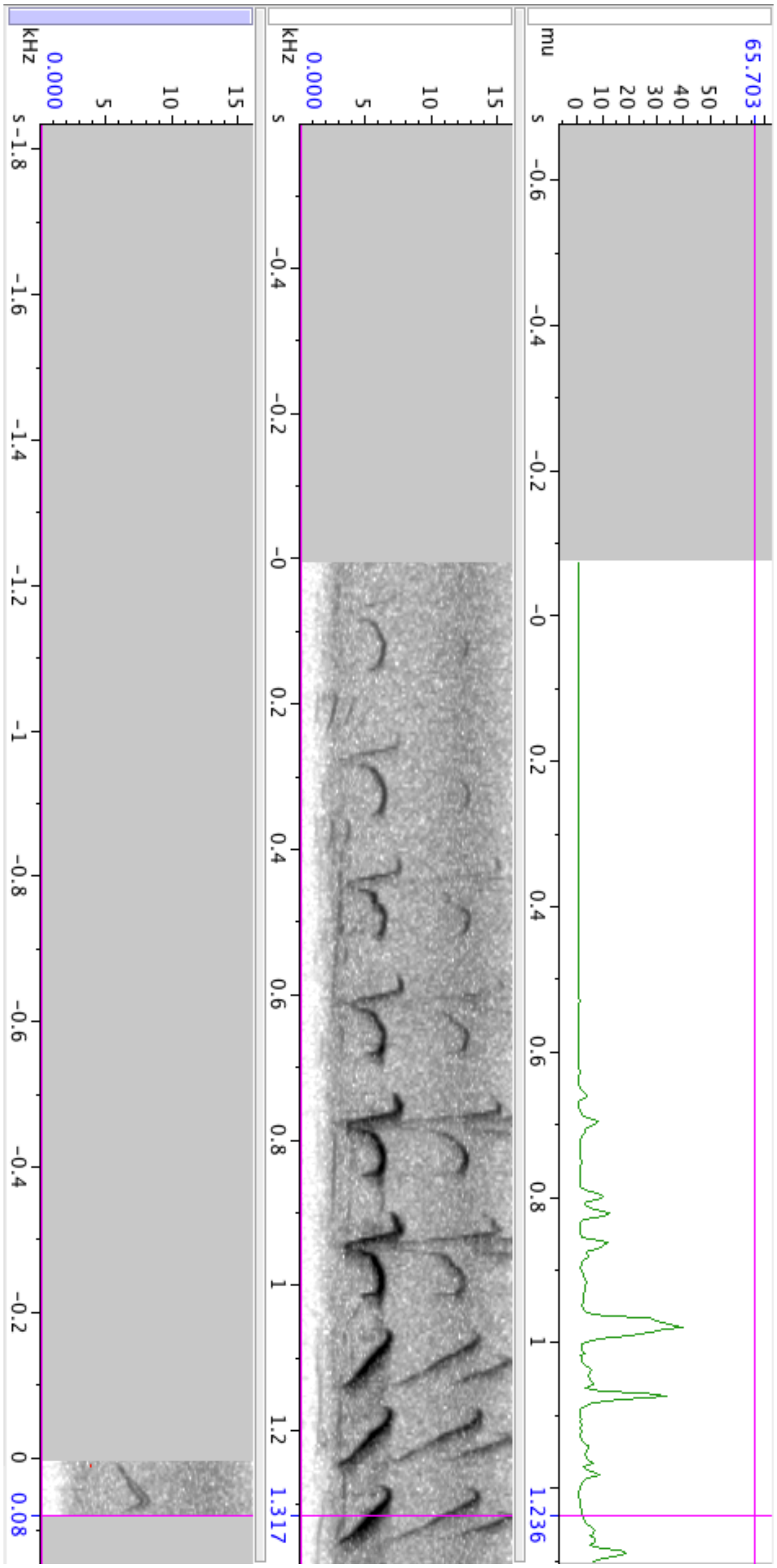


Figure 4.


65.703
60
50
40
30
20
10
0
mu
s
-0.6
-0.4
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-0
0.2
0.4
0.6
0.8
1
1.236
kHz
0.000
5
10
15
s
-0.4
-0.2
-0
0.2
0.4
0.6
0.8
1
1.2
1.317
kHz
0.000
5
10
15
s
-1.8
-1.6
-1.4
-1.2
-1
-0.8
-0.6
-0.4
-0.2
0
0.08

Finding Yellow Warbler nests on Kent Island

Sexual dimorphism and confusing species

Yellow Warblers are sexually dimorphic, so differentiating males and females was easy. Males are bright yellow with rusty red-brown streaks on their breast and they sing. Females are a drabber yellow and did not sing, although they did chip. Occasionally, females had very light streaking, but they were still easily distinguished from males. I found American Redstart songs sounded like the beginning of Yellow Warbler songs. The chips of the two species also sounded similar, but Redstarts were usually found in denser, forested environments. The two species mixed and sometimes interacted on forest edges. At the beginning of the Kent Island season, I confused migrant Wilson's Warblers with female Yellow Warbler. During the summer, I occasionally confused Alder Flycatchers with females as well, but the two species behaved differently, so brief observation quickly differentiated the species. Males arrived before females during the 2015 summer. The early arrival provided a good opportunity to learn the song (and its many variations) in the field and to observe initial territory establishment.

Timing

Having a general knowledge of ecology and timing would have been helpful in finding nests and predicting female behavior. I first observed nest building behavior on 29 May, and next on 30 May, but late females continued to build their first nests until 9-10 June. The first successful eggs were laid on 3 June. Late females laid their first eggs on 11-12 June. One female who renested after depredation laid her first egg of the second nest on the 26 June, one week after losing the previous nest. While day-to-day timing probably differs from year to year, this should provide an approximate range for observing nest building/ incubation behavior. Nestlings first hatched on 18 June.

Determining territories

Before finding nests, it was useful to determine the males' territories because these were the areas in which females built nests. Walking around the island on the first 3 or 4 days sufficed for getting a general sense of where territories were, but color banding males would have helped with specific determination. I found traversing the forest edge to be a helpful way of learning about territories and habitat. Yellow Warblers nested primarily in open areas, but they are usually near a forest edge because the fledglings took shelter in forested areas once they are able to. Walking the forest edge meant extensive bushwhacking, but it was a helpful and comprehensive way to males and most of the territories.

Macroenvironment

Yellow Warblers foraged on forest edges in spruce groves, but they almost always nested in open environments, sometimes more than 100 meters from where a male foraged and sang. Territories were about 100-150 meters in diameter and were be found all over the island (although not in the field extending to South Hill). However the northern half was more densely populated. I found gooseberry shrubs on the shore edge to be the easiest environment in which to find nests because females were easy to track. Females spaced out their nests by about 150 yards along the shore, which was similar to the distribution of singing males. I found females nesting in gooseberry along the north and west shores of Kent Island. Females also nest in raspberry bushes, although seemingly preferred gooseberry or ferns. Fern nests were hard to find because they were often in the middle of larger, homogenous fern patches. I was careful approaching fern nests to avoid accidentally stepping on them. The females that nested in ferns did not to stitch two plants together, so walking between plants, rather than over them, was safer. Fern nesting females were found northwest of the Shire, in the Eagle Nest region, in the northern tip of the island, near the main building, and towards the southern tip of continuous forest along west shore. I also found one female nesting in the space underneath a fallen tree.

Approach

Finding Yellow Warbler nests took patience. In any stage, I first found an individual, preferably a female, and waited for it to behave in a way that indicated where the nest was. I always watched from a distance, usually using binoculars, to let the warbler behave normally. I also tried to pick spots that allowed me the best big picture vantage point in case the warbler flew off. When I got too close to the nest, females chip chipped at me and did not return to the nest. However, if you step back sufficiently, she will likely return to her nest. In general, I looked for the female to return to the same spot repeatedly. When I was confident, I approached, searched, and left after about five minutes to avoid disturbing the female too much.

Locating the nest

It was sometimes much easier to find the nesting vicinity than the actual nest. Females entered the nest area about a meter away from the nest and usually could not be seen returning to the actual nest, unless I already know where the nest was. When I had a strong idea as to the nest’s location, I approached the spot and either flushed the female or spent a couple minutes searching through the area by prying back branches or ferns.

They are usually knee height, or a little higher. I think it would have been helpful to familiarize myself with images of Yellow Warbler nests before trying to find them.

There are three stages of breeding development in which to find nests: the nest-building stage, incubation, and nestling feeding.

Nest building

Finding the female is much easier at this stage. I looked for females carrying nest material such as plant down from fire weed, straw, or feathers in her bill. When females were nest building, they made a trip to the nest with material every 2-3 minutes and repeated this five to six times before taking a five to ten minute break to forage. Females who started early in the season took up to a week to build their nests, but late females or females who lost nests built them in about two to four days. When finding a nest in this stage, it was helpful to note the exact area of building and then come back to search for the nest a day or two later. Checking later allowed further nest development, making the nest easier to find, and I think spreading my search over several days was less disturbing to females. Males were not that useful during nest building. Late in nest building, males mate guarded pretty heavily, but they rarely flew to the nest with the female. Furthermore, copulation occured near the end of nest building, so males were still competing with each other for territories and females as the females built. They often sang during this period, although they sometimes whisper sang or chipped when the female was away from the nest.

Incubation

During incubation, I used the female or the male to find a nest. Female incubation patterns are pretty regular (about 12-20 minutes on, 5-10 minutes off), so the female generally returned to the nest soon after being seen off of it. Females often chipped while off the nest and males mate-guarded during incubation, so I often used vocalizations to locate individuals. If I found a female incubating an incomplete clutch, I could estimate the day on which the first egg was laid. Incubating females seemed to forage frantically, spending no more than a second on any particular perch. Females also did not forage far from their nest, so I was able to easily track females back to their nest site. Females also waited until I was very close to the nest to flush. When I followed females back to their nest site after an incubation bout, I was able to get an exact nest location by waiting about a 1.5 minutes to let the female settle, then approaching the general nest spot, sweeping the vegetation above the suspected nest location, and watching to see where the female left from. Males also fed the females during incubation. Males carrying food almost always led me to the nest.

Nestling feeding

Both males and females fed nestlings. Females brooded 1-day-old and 2-day-old nestlings, but they also made foraging trips and brought food back to the nest. The males made frequent trips to the nest with food, usually once every two to three minutes. As the nestlings matured, both the males and females made frequent trips to the nest. I found the males' trips easier to follow during feeding. Males almost always sang either right before entering the nest or right after exiting, which meant listening to their songs could help narrow down the nest location. Furthermore, males made more conspicuous trips and usually perched near the nest before entering, while females flew more subtly and often concealed themselves in shrubs. Although begging calls of 3-day-old nestlings were audible, they for not helpful for finding nests because they were too quiet to hear without headphones and a microphone.

Renesting

Females who lost nests began building another soon after. Females nested within about 100 meters from their original nest. Males appeared compete again for the female after she lost a nest. One female seemed to try several nest spots, depositing material in more than one area, which made finding the nest at the beginning of building more difficult.

Marking nests

For nests I spent a lot of time finding, I did not need to mark them. By returning to them frequently, I learned landmarks near the nest and had a very good sense of its exact location. I also did not find enough nests to forget where they were. I did mark nests in ferns with a small bit of flagging tape above or near the nest because fern environments tend to be homogenous. I also marked nests that I did not find.

Mapping nests

I mapped the nests on a Kent Island template to inform my future searches, as nests were fairly evenly distributed along the forest edge. Mapping also allowed me to use the transect lines to refer to nests. These are constant and provide a way of consistent method of nest documentation.