

Early singing onset in the black-cheeked gnateater (*Conopophaga melanops*)

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ABSTRACT: Early singing onset in the black-cheeked gnateater (*Conopophaga melanops*). Song learning in birds has been intensively studied, mostly in the suborder Oscines. While studying the black-cheeked gnateater *Conopophaga melanops* (Suboscine) in southern Brazil nestling vocalizations were observed. Adult and nestlings vocalizations were described and compared to examine age-specific variation in song structure. Nestling vocalization was more similar to adult song than to alarm calls. However, nestling and adults songs differed primarily in maximum frequency and total length of the song. Nestling age was also correlated with some nestling song features. These patterns suggest that while vocalization at an early age may be innate, nonetheless, there may also be a stage during which individuals could learn the adult song. Because this early song is not the same as the adult song, we suggest that some Suboscines may achieve their song only after practice, although not necessarily with an imitative-learning basis, such as in Oscines. Further study will be required, with observations beginning with young birds on the nests, to better understand the ontogeny of song and individual variability in adults Suboscines.

KEY-WORDS: Conopophagidae; innate behavior; learning; Suboscine; vocalization.

INTRODUCTION

Questions about the development of avian song learning have a long history of debate (Marler & Tamura 1964, Nottebohm 1970, Immelmann 1975). One general pattern is clear in which some songbirds, parrots, and hummingbirds learn from imitation (Gaunt *et al.* 1994, Farabaugh *et al.* 1994, Berg *et al.* 2011) while other birds inherit song templates (Kroodsma 1984, Kroodsma & Konishi 1991). Oscines (songbirds, suborder Passeri), the best studied group, may learn and modify their songs over time (Marler & Tamura 1962, Chaiken *et al.* 1994, Brenowitz & Beecher 2005, Kirn 2010), while the Suboscines (the other passerines, suborder Tyranni) are poorly studied and thought to have innate songs that are relatively unmodified over time (Kroodsma 1984). Although this pattern is widely accepted, more empirical and experimental data are available for those species that “learn” than there is for the non-learners, the Suboscines (and others). However, learning may be more common than thought, even among the Suboscines (Leger 2005, Saranathan *et al.* 2007).

In those species that learn songs, young birds pass through a sensitive period during which they acquire information that will shape song development. In some

species, song learning occurs at a certain age, while others may learn at any age (Nottebohm 1970, Farabaugh *et al.* 1994, Tramontin & Brenowitz 1999). The learning stage (involving auditory and recording mechanisms prior to song production) usually begins the first month after hatching and may continue through the first year (Kroodsma & Konishi 1991, Marler 1997, Brenowitz & Beecher 2005). In most species within the Suboscines, when singing begins and when the song acquires the adult form are unknown. Although they are not expected to go through a typical song-learning phase, it is unlikely that the first vocalizations of a young bird will be that of an adult song (Kroodsma 1984).

The Atlantic Forest endemic black-cheeked gnateater *Conopophaga melanops* (South American bird family Conopophagidae) is a tracheophone Suboscines (Irestedt *et al.* 2002). This gnateater is a socially monogamous and territorial species, and in general has life history traits more related to slow pace species (Wiersma *et al.* 2007). Such traits would include an extended nest cycle, low clutch size and extended parental care. As example, the nest cycle may take more than 50 days since the nest building (Lima & Roper 2009a).

While studying the population dynamics of the black-cheeked gnateater in southern Brazil (Lima &

Roper 2009a), an unusual nestling singing behavior was observed. While based on few and sporadic observations, the lack of knowledge on song ontogeny within the Suboscines suggests that our information may be useful to better understand such process. Thus, we describe and compare adult and nestling vocalizations to discuss a first approach on the song development in this Suboscine passerine.

METHODS

The black-cheeked gnatcatcher *Conopophaga melanops* was studied at a Private Reserve located in the municipality of Guaraqueçaba, state of Paraná, southern Brazil (25°13'S, 48°17'W). The reserve is at the lowland and mountain tropical forest, comprising approximately 2300 ha, in a larger matrix of mixed successional forest stages (> 400 000 ha) contiguous with the largest area of well-preserved Atlantic Forest. We captured and monitored gnatcatchers in a 25 ha plot (Lima & Roper 2009a).

Nestlings were observed and monitored at five of 18 nesting attempts. Some nestlings (three individuals in two nests) were observed as they occasionally vocalized. In eight observations, vocalizations were digitally recorded (Tascam DR08 with an external microphone Sennheiser ME66). Also, digital videos were recorded twice of singing nestlings on the nest (Sony DSC/H2). Songs of the three nestlings were recorded from 2-4 times on different days (thus, diverse ages). Nestling age was estimated based on the last date eggs were found and in comparison with nests found before hatching. Songs of adult males were recorded in the field (N = 10). One song per adult was used.

Sound was analyzed in Raven Lite 1.0 (Cornell Lab of Ornithology, USA). Audio spectrograms were compared among nestlings and adults. Acoustic parameters used for comparison include total length (s), note rate (s⁻¹), and fundamental frequency range (kHz), measured as the maximum and the minimum frequencies at two moments of each song: after the first second (f1) and at the beginning of the last second (f2) (i.e., a song that last 8.3 s had frequencies measured at 1.0 s, as f1, and f2 at 7.3 s). Adult and nestling song features were compared using *t* tests and regression analysis. We carried out regression analysis for checking the correlation between nestling age and song features. Tests were considered statistically significant when $P \leq 0.05$.

RESULTS

Adults sing a long and multi-note song (mean + SD = 9.3 + 0.8 s, with 12.2 + 0.2 notes s⁻¹, n = 10, Figure 1). Adult song had usually presented two or three

harmonics, with the lower frequency harmonic ranging around 2.7 – 4.2 kHz (f1_{max} + SD = 3.5 + 0.2 kHz, and f2_{max} + SD = 4.0 + 0.3 kHz, n = 10). The two succeeding harmonics ranges around 4.7 – 5.7 and 6.2 – 7.7 kHz. A unique recording presented four evident harmonics, which was the only one including the harmonic with the lower and fundamental frequency (1.5 – 1.9 kHz), with a second and dominant harmonic around 2.8 – 3.9 kHz. Comparisons of initial and final frequencies were possible for the dominant harmonic, which increased the modulation toward the end of the song (f1_{min-max} = 2.7 – 3.7 kHz, f2_{min-max} = 3.3 – 4.2 kHz, r = 0.49, df = 9, P < 0.05). The alarm call is quite different than the song (Fig. 1) and it is a single short pulse (~ 0.2 s) with a high and broad frequency (3.2 – 16 kHz).

The nestling emits a similar but shorter song (mean + SD = 3.9 + 0.3 s, 12.2 + 0.6 notes s⁻¹, n = 8; Figure 1). Nestling songs start and finish at lower frequencies than those of adults (f1_{max} + SD = 2.8 + 0.2 kHz, *t* = 4.08, P < 0.05, and f2_{max} + SD = 3.4 + 0.2 kHz, *t* = 6.5, P < 0.05), and there is an increase in the modulation throughout the song for nestlings (r = 0.84, df = 7, P < 0.05). Only one harmonic, at 4.7-5.9 kHz, were found in one recording (from the older nestling in the sample, with the higher maximum frequency in figure 2). The emission of the sound was in apparent response to approach, during which the nestling stayed in the usual nestling posture. During sound emission, the body of the nestling vibrated in synchrony with the sound (we can send the video file for those interested). Begging was never seemed during observations of parental care at five nests where nestlings had survived (Lima e Roper 2009a). No other sounds were noted, even when nestlings were manipulated (for banding).

The age of nestlings was estimated for one nest found on 10 December 2006 with two eggs that by 12 December had hatched. The first juvenile observed singing in that nest was on 22 December (at 10-11 days after hatching). Another nest was found with two chicks on 12 January 2007, and when compared to nestlings of known age, they were estimated to be 8 days old. One nestling were recorded singing when the nest was found, and then, both nestlings “sang” in three (13, 18 and 23 January) of six observations before they fledged on 25 January, a date that corroborate with the estimated age (Lima & Roper 2009a). Thus, the age of nestlings at this nest was 8 and 9 days after hatching when was it found.

Nestling age was correlated with some characteristics of the song. Maximum frequency at the end of the song (f2) and nestling age were correlated (r = 0.83, df = 7, P < 0.05, Figure 3). Total song length and age were correlated (r = 0.64) but at n = 9, P = 0.07. Minimum and maximum frequencies at the beginning of the song (f1) were independent of nestling age.

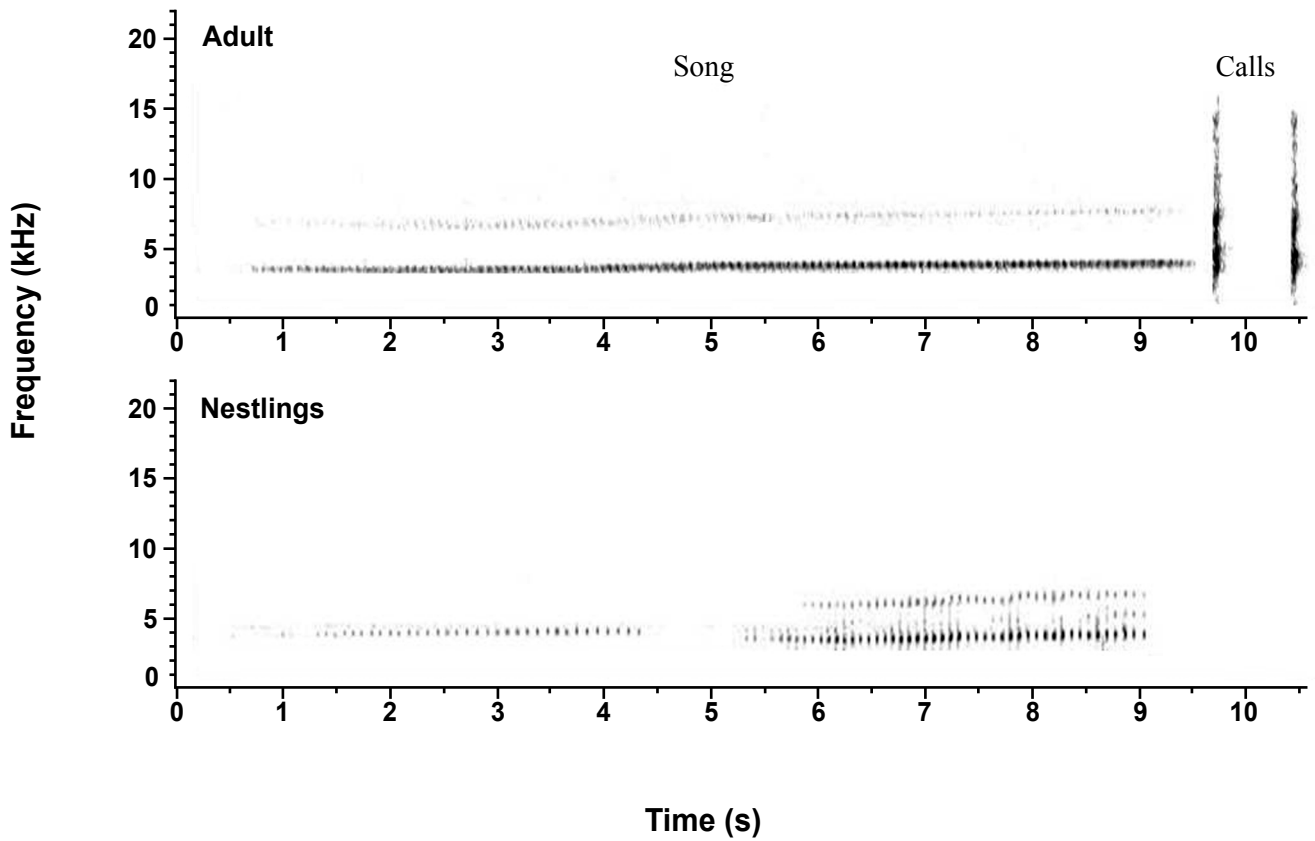


FIGURE 1. Song and call spectrogram of the adult black-cheeked gnateater *Conopophaga melanops*, and the audio spectrogram of two nestlings.

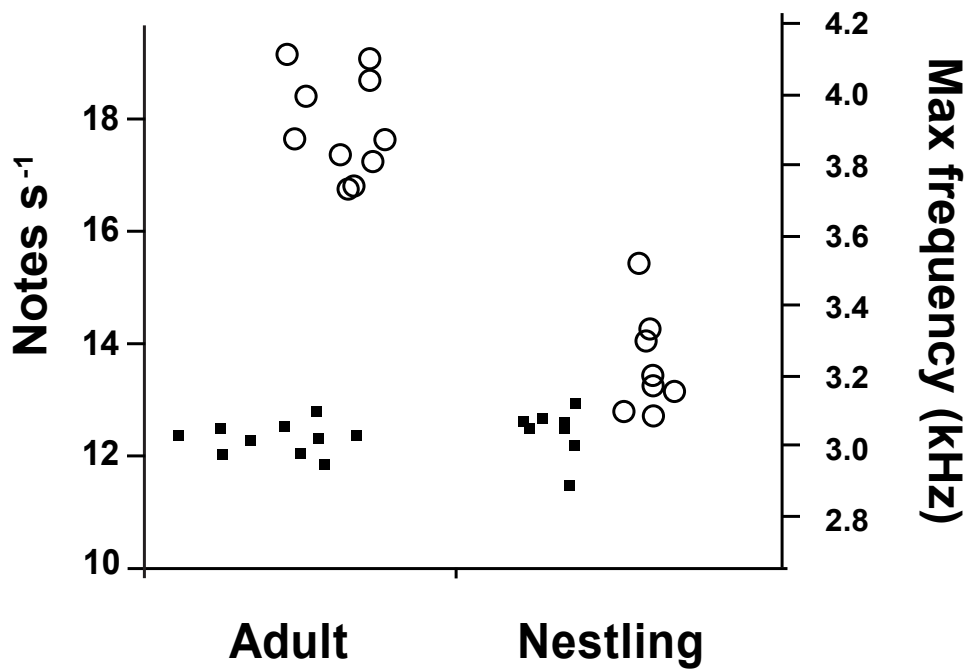


FIGURE 2. Song features points for adults and nestlings of black-cheeked gnateater *Conopophaga melanops*: black dots show note rate and white circles show maximum frequency (kHz).

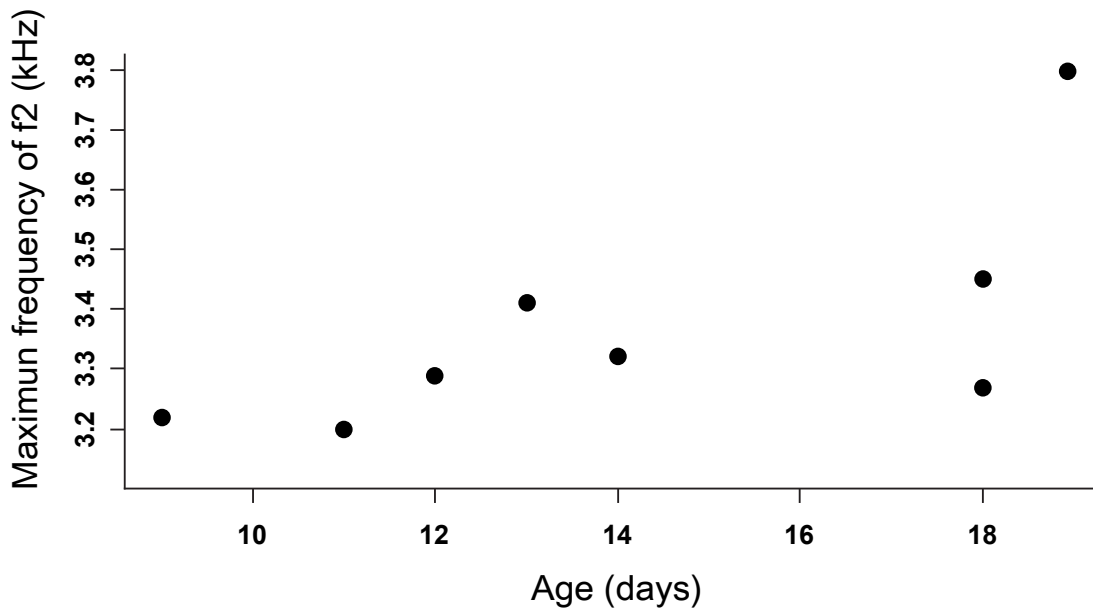


FIGURE 3. Correlation between maximum frequency (kHz) in the end of the song (f_2) and the age (in days) of nestlings of black-cheeked gnatcatcher *Conopophaga melanops*.

DISCUSSION

Nestling vocalizations always more closely resembled adult songs than they did begging or alarm calls. This was somewhat surprising because vocalizations seemed to be in response to our approaching the nest, and so might have been in alarm. Or, perhaps the noise we made suggested to the bird that adults were returning with food. Despite of the reason they sang, the similarity between adult and young songs suggests that a song template is inherited, as expected for Suboscines (Kroodsma 1984, Kroodsma & Konishi 1991), but which must be improved as the nestling grows.

Nestling black-cheeked gnatcatchers begin to sing earlier than other not related species (Kroodsma & Pickert 1984, Podos *et al.* 2004). Furthermore, some features of the song seem age-dependent. The maximum frequency of the dominant harmonic increased with age approaching that of the adult song, while young birds remained on the nest (Figure 3). A similar process goes through the total length of their song (Figure 1). This appears to be learning on the part of the young black-cheeked gnatcatcher and which would aim to result in an adult song with respect to frequency and song length. Thus, while nestling black-cheeked gnatcatchers inherit a song template, apparently the song is being practiced since early age such that learning may be involved to “fine-tuned” the song into that of an adult (such as longer duration and higher frequencies).

Such fine-tuning may be due to the young bird comparing its own song with that of the adult singing nearby (Leger 2005, Saranathan *et al.* 2007). Or also, it

may be due to the young bird comparing its own song with some innate “template”, because nestlings can sing similar to an adult prior to leaving the nest. This could be also somehow associated to the fitness or the body developmental rate of each individual, such as an age-dependent tonus of the syrinx’s muscles, or the body (and vocal tract) size (Marler 1997, Podos *et al.* 2004, Cardoso 2010).

Nevertheless, even if the song ontogeny does not include any auditory feedback-imitation, the song of young birds did not entirely fit as an adult song. As adult songs presents some variation in the maximum frequency, and the song has an ascendant modulation, potential song individual variability would likely appears in adults by differences in the frequency level in the end of the song, and perhaps either in the song duration. Thus, it is likely that grown-up individuals will not achieve exactly the same song features when adults (Lampe & Espmark 1994, Nelson & Marler 2005, Berg *et al.* 2011), even being a Suboscine species (Ippi *et al.* 2011).

We suspect that learning may be more broadly correlated with song ontogeny here than previously thought. This could be potentially important for this species, due to the role of the song as a territory-maintenance device (Lima & Roper 2009a, b). If so, then social context, phenotypic and environmental variation may also influence song development in this and perhaps several others Suboscine species, but not essentially as it does in the Oscines (Mace 1987, Hoi-Leitner *et al.* 1995, Nowicki *et al.* 2002, O’Loghlen & Rothstein 2002, Kojima & Doupe 2011).

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