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SONG LEARNING IN THE RUFOUS-COLLARED SPARROW (*Zonotrichia capensis*)

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SUMMARY. The role of learning in the development of the Rufous-collared Sparrow's song was investigated comparing the primary song of 10 subjects captured at different ages and raised in acoustic isolation or trained with conspecific tape-tutors. The subjects captured before day 10 of age and deprived of song models developed abnormal songs, lacking introduction (theme) and trill. In contrast, subjects captured and isolated after day 35-40 of age developed good copies of the song of their natal population. These facts suggest that the acoustical experience with the song from their natal area is sufficient for the imitation of their natal dialect. Subjects captured as nestlings and tape-tutored with natal and alien dialects developed songs with some features of the models, indicating the importance of the early acoustic experience in development of song. No evidences of song copying were found when tape-tutoring started after day 40 of age.
Key words: song learning, Rufous-collared Sparrow, *Zonotrichia capensis*, imitation, dialect.

Aprendizaje del canto en el chingolo (*Zonotrichia capensis*)

RESUMEN. Se investigó el papel del aprendizaje en el desarrollo del canto del chingolo, mediante la comparación de los cantos primarios desarrollados por 10 sujetos capturados a diferentes edades y criados en aislación acústica o entrenados con tutores grabados conespecíficos.

Los sujetos capturados antes de los 10 días de vida, y privados de modelos de canto para escuchar, desarrollaron cantos anormales, carentes de introducción (tema) y trino. En contraposición, los sujetos capturados y aislados a partir de los 35-40 días de vida desarrollaron buenas copias de los cantos de su población natal. Estos hechos sugieren que la exposición a los cantos de los adultos del área donde se crían los pichones es suficiente para la imitación del dialecto. Los sujetos capturados y expuestos tempranamente a grabaciones de canto, desarrollaron cantos con algunas de las características del modelo utilizado, lo cual muestra la importancia de la experiencia acústica temprana en el aprendizaje del canto. No se hallaron evidencias de la copia del tutor grabado con posterioridad a los 40 días de vida.
Palabras clave: aprendizaje del canto, chingolo, *Zonotrichia capensis*, imitación, dialecto

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INTRODUCTION

The Rufous-collared Sparrow (*Zonotrichia capensis*) is a common species in open and semi-open habitats throughout Latin America. The song of this species has two parts: an introduction and a final portion, referred to as "theme" and "trill", respectively (Nottebohm 1969). In some populations of Costa Rica and northwestern Argentina the trill may be absent (Nottebohm 1975, Handford & Lougheed 1991, Fotheringham 1995). The theme is usually composed of 2 to 5 whistled ascending or descending notes (Handford & Lougheed 1991). According to the number, shape and ordering of the notes, it is possible to distinguish different themes. In subtropical and temperate populations, within an area, each male sings a single theme (rarely two), although some themes are shared by several neighboring individuals forming local "theme mosaics" (King 1972). On the other hand, trill interval (time between consecutive notes in the trill) is relatively constant within an area, but it changes among life zones, thus giving rise to habitat-related regional dialects (Nottebohm 1969, King 1972, Nottebohm 1975, Handford & Nottebohm 1976, Handford 1981, 1988, Lougheed *et al.*, 1989, Tubaro *et al.*, 1993, Tubaro & Segura 1994).

Since song sharing and dialects are often products of intraspecific vocal imitation (Kroodsma 1982, Mundinger 1982), the above described patterns of song variation in *Z. capensis* suggest that theme and trill features might be learned in this species. In accord with this view, Egli (1971) hand-raised two nestlings from about five days of age, and found that they developed the alien song heard from a wild tutor during the following month, rather than their natal dialect. Although this preliminary experiment suggests that *Z. capensis* imitates the songs of conspecific males during an early sensitive period, this finding is not conclusive since: a) experimental subjects could have had experience in their natal area with the alien song that they finally developed (because they hatched near the dialect frontier and their putative father included the alien song in its repertoire), and b) the experiment did not include an acoustically isolated group to control for the effect of rearing conditions on song development. In this study we investigate the role of learning in *Z. capensis* song development, by comparing the primary song of subjects captured at different ages and raised in acoustic isolation or tape-tutored with conspecific song models.

METHODS

Ten *Z. capensis* individuals were tested in these experiments. Six fledglings (M548, M107, M228, M550, M549 and M217) were captured during November 1988 (estimated age of 35 days from hatch) at the Elsa Shaw de Pearson Reserve (Estancia El Destino, 35° 05' S, 57° 31' W), Partido of Magdalena, Buenos Aires Province, Argentina. The other four (L024, L184, L469, and L004) were captured as nestlings of about 5-8 days of age, during December 1988 and January 1990, at the Campus of the Luján University (34° 34' S, 58° 06' W), Partido of Luján, Buenos Aires Province.

Birds captured at Magdalena came from the "Talar" dialect population, while the Luján ones came from the "Steppe" dialect population. Talar dialect has a longer trill interval [TRINT, $\bar{x}$ = 90 ms, S.D. = 6 ms], fewer trill notes [TN, $\bar{x}$ = 5.87 notes, S.D. = 1.99 notes], and lower minimum trill frequency [TRMIN, $\bar{x}$ = 3200 Hz, S.D. = 100 Hz] than Steppe dialect [TRINT, $\bar{x}$ = 62 ms, S.D. = 19 ms; TN, $\bar{x}$ = 7.34 notes, S.D. = 3.21 notes; TRIMIN, $\bar{x}$ = 3600 Hz, S.D. = 100 Hz] (Tubaro 1990, Tubaro *et al.*, 1993). All subjects were communally hand-raised in the laboratory and exposed to the natural summer photoperiod. At the age of 40 days all subjects were completely independent of care, and housed in individually sound-proof chambers, with a photoperiod of 16 h of light and 8 h of darkness.

In the tutoring procedure, tape loops containing the song stimulus were played

through a Uher 4000 Report L connected to a speaker mounted inside each sound proof chamber. The length of the loop was calculated to produce a silent interval between two consecutive songs of about 9 s, an interval frequently used by wild birds in their song bouts (Tubaro 1990). In order to reduce habituation to the song stimulus, each playback session lasted only six minutes, and was followed by a period of silence of the same duration, throughout the light hours.

Four individuals captured as fledglings from Talar (M548; M107; M228; and M550) received 24 days of song-tutoring, beginning when they were 40 days old. They were exposed to about 100000 repetitions of a typical song of Capilla del Monte dialect (trill interval = 30 ms, number of trill notes = 11, minimum trill frequency = 4000 Hz; see Fig. 1). This dialect occurs in the mountains ranges of Córdoba Province, about 800 km from the place where subjects were hatched, thus avoiding the possibility that they could have ever heard this song in their natal area.

Two individuals captured as nestlings from Steppe (L469; L004) were trained between day 22 and 31 of age with fewer than 6000 repetitions. L469 experienced a typical song of Talar [trill interval = 117 ms, number of trill notes = 3, minimum trill frequency = 3200 Hz], while L004 experienced the Steppe dialect [trill interval = 53 ms, number of trill notes = 8, minimum trill frequency = 3700 Hz] (see Fig. 1). These stimuli were presented during eight two-hour playback sessions, starting in the afternoon. The silence interval between two consecutive stimuli ranged from 7 to 9 s. For this treatment each subject was individually placed in a sound proof chamber. The rest of the day both subjects remained in adjacent wire boxes.

Finally, the last four individuals (two captured as nestlings from Steppe [L024; and L184], and two captured as fledglings from Talar [M549; and M217]) were maintained acoustically isolated during all the experiment.

The songs of each individual were sampled using a voice-activated tape-recorder connected to a microphone placed in the ceiling of the sound proof chamber. Individuals were sampled during one or two days each two weeks until they were about one year old. In addition, each chamber was sampled by ear for 15-60 minutes a week to detect songs of low amplitude which could not reach the activating threshold of the automatic recording system. Sonograms were

Table 1. Summary of the experimental design, including a list of subjects studied, aspects of tape-tutoring, and song developed.

Subject	Natal dialect	Age captured [a]	Tutor-songs	Number of songs received	Age tutored [a]	Primary song developed
M548 [bc]	Talar	35	Capilla del Monte	>100000	40-64	None
M107	Talar	35	Capilla del Monte	>100000	40-64	Partial [d]
M228 [b]	Talar	35	Capilla del Monte	>100000	40-64	Talar
M550	Talar	35	Capilla del Monte	>100000	40-64	Talar
M549 [bc]	Talar	35	None	None	None	Talar
M217	Talar	35	None	None	None	Talar
L024	Steppe	<10	None	None	None	Abnormal
L184 [b]	Steppe	<10	None	None	None	Abnormal
L469	Steppe	<10	Talar	< 6000	22-31	Talar-like [e]
L004	Steppe	<10	Steppe	< 6000	22-31	Steppe-like [e]

[a] age in days. [b] females. [c] implanted with a pellet (15 mg) of testosterone propionate. [d] only introduction, but similar to that of its father. [e] only with some resemblances to the tutor song (i.e. presence of a sketchy theme and trill, the latter with trill interval and minimum trill frequency like the tutor song).

made from tape-recordings using a Kay Elemetrics Sonagraph 7029-A, set for wide band filters and the 80-8000 Hz frequency range. All but subject M548, came into song during the course of the experiment, one of them after implantation with a pellet of testosterone propionate (15 mg). Post-mortem autopsies of the experimental subjects revealed that four of them were females. Table 1 summarizes the sex, treatment received, and song developed by each subject.

In order to assess the quality of the song developed by experimental subjects, we visually compared their sonograms with those of their putative fathers, tape-tutors, and those of neighboring males from the natal area.

RESULTS

SONG DEVELOPED BY ACOUSTICALLY ISOLATED BIRDS

There were striking differences between the song developed by subjects captured as nestlings and the song developed by subjects captured as fledglings (Fig. 1). The former (a male and a female) developed abnormal songs lacking a recognizable theme and trill parts, and thus, without the acoustic features that define their dialect (or even their species) affiliation. These songs were highly variable in structure and had notes of a quavering quality. Female L184, gave songs which were two or three times longer than

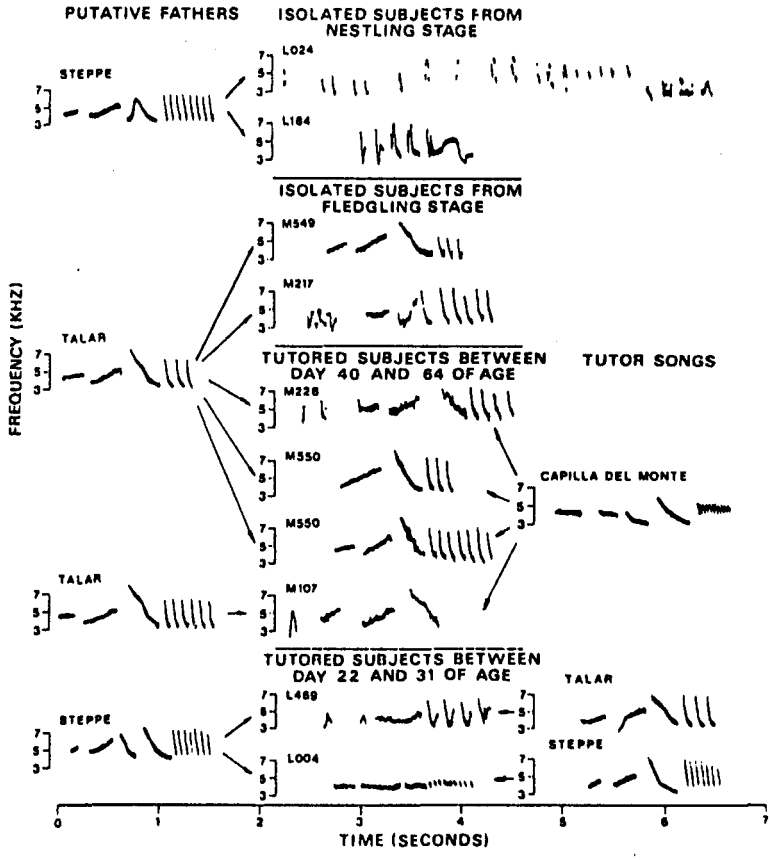

Figure 1. Songs developed by the experimental subjects, compared with those of their wild fathers and tape-tutors. Arrows point from fathers to their sons, and from tutors to their pupils. Codes on sonograms correspond to subjects' code in Table 1. Note important individual differences in the song produced by the different subjects.

normal ($\bar{x}$ = 3.69 s, S.D. = 1.14 s, N = 9 songs).

In contrast, birds captured and isolated as fledglings developed normal songs with a theme and a trill. In particular, their trill features were similar to those of Talar dialect as well as those of their putative father (see Table 2 and Fig. 1).

SONG DEVELOPED BY TAPE-TUTORED BIRDS

Three out of four birds tutored between Day 40 and 64 (two males and a female) developed songs, and only two of them (M228 and M550) sang complete songs with theme and trill. These songs had no obvious resemblances to the tutor song (Fig. 1), but fell well into the range of variation of their native Talar dialect (Tubaro 1990, Tubaro *et al.*, 1993). In addition, subject M550 sang a repertoire of two song types, one starting with a two-note theme, and the other with a three note one. Throughout the study period, the three-note theme was progressively eliminated from its repertoire.

The two birds (L469, and L004) tutored before Day 35, developed abnormal songs, but with some resemblances to the tutor song (see Fig. 1 and Table 2). In particular, bird L469 sang songs that were similar to the Talar tutor song in trill interval, but different to the songs of its Steppe putative father (see Table 2). The song of subject L004 was similar to the "isolated" song reported in some *Z. leucophrys* subjects raised in laboratory (Baptista & Petrinovich 1984, Petrinovich 1985), in that it was composed of a number of notes of sustained frequency. The songs did however retain the two-part structure of *Z. capensis* song. If we accept that the last part of these songs is a trill, it is then interesting to note the similarity to its Steppe tutor model in their short trill interval (see Fig. 1 and Table 2).

DISCUSSION

The presence of normal songs in subjects captured as fledglings and their absence

Table 2. Means ± standard deviation for three trill features of the experimental subjects and their putative fathers.

	Isolated subjects from fledgling stage				Father	
	M217	N [c]	M549	N	N	
Number of notes	2.58 ± 1.00	(12)	3.20 ± 1.14	(10)	2.25 ± 0.89	(8)
Trill interval [a]	95 ± 20	(10)	97 ± 14	(10)	109 ± 3	(6)
Minimum frequency [b]	3100 ± 300	(12)	2800 ± 300	(10)	3200 ± 100	(8)
	Tutored subjects between day 40 and 64 of age				Father	
	M228	N	M550	N	N	
Number of notes	4.00 ± 1.41	(10)	5.00 ± 1.05	(10)	2.25 ± 0.89	(8)
Trill interval	121 ± 14	(9)	92 ± 3	(10)	109 ± 3	(6)
Minimum frequency	2700 ± 300	(10)	3300 ± 100	(10)	3200 ± 100	(8)
	Tutored subjects between day 22 and 31 of age				Father	
	L469 (Talar tutor)	N	L004 (Steppe tutor)	N	N	
Number of notes	3.71 ± 1.25	(7)	6.88 ± 3.56	(8)	6.90 ± 2.42	(10)
Trill interval	151 ± 21	(7)	55 ± 6	(8)	55 ± 2	(10)
Minimum frequency	3300 ± 200	(7)	3600 ± 200	(8)	3800 ± 100	(10)

[a]: in milliseconds; [b]: in Hz; [c]: number of songs analyzed.

in subjects captured as nestlings when all were raised in acoustic isolation, suggests that experience with adult song occurring between the second and the seventh week, affects the song developed by *Z. capensis*. Similarly, in *Z. leucophrys nuttalli* it has been shown that song acquisition may occur very early in life, and a fledging as young as 28 days old was reported singing an almost crystallized song (Baptista *et al.*, 1993). For *Z. capensis* males, the existence of an early period of song learning is supported by the presence of some tutor features in the songs developed by nestlings reared in laboratory and trained with song playbacks before Day 35 (L469, and L004).

In contrast, we did not find any conclusive evidence of song copying when tape-tutoring started after Day 40. These results, however, do not imply that the experience after Day 40 is not important in song development. Several studies in White-crowned Sparrow (*Z. leucophrys*) have shown that the use of social tutors could extend the duration of the sensitive period of vocal learning, and even allow the copying of allospecific song patterns (Baptista & Petrinovich 1984, 1986, Petrinovich & Baptista 1987). In addition, acoustic and social experiences later in life may be responsible of the selective attrition of song variants produced during the plastic stages of song development (Marler & Nelson 1993, Nelson & Marler 1994).

In spite of the fact that wild females do not sing or sing rarely (King 1972), two experimental females sang spontaneously, and an additional one after being implanted with a pellet of testosterone propionate. In particular, females captured at Day 35 sang good copies of their natal dialect, suggesting that they had learnt the acoustic features of their natal population. Whether this learning affects female's sexual preferences is not known, although this possibility contributed significantly to the initial scientific interest in *Z. capensis* dialects (Nottebohm 1969. Handford & Nottebohm 1976, but see Chilton *et al.*, 1990, Lougheed *et al.*, 1993). Why did tape-tutored birds fail to learn exact copies of the tutor song? We cannot at this time answer this question, but social interaction could be necessary for an accurate copy of the model. This idea is consistent with data on Indigo buntings (*Passerina cyanea*), Canaries (*Serinus canarius*) and Galapagos finches (*Camarhynchus parvulus*) in that some learning occurs with tapes, but living birds are more effective tutors (for a review see Baptista & Gaunt 1997). In addition, 6000 songs might not provide enough experience, although studies on *Z. leucophrys* indicate that tutor song can be learned with as few as 120 or 252 presentations (Petrinovich 1985).

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