Ethology **109,** 55—66 (2003)

ISSN 0179–1613

Changes in Song Complexity Correspond to Periods of Female Fertility in Blue Grosbeaks (*Guiraca caerulea*)

Barbara Ballentine, Alexander Badyaev & Geoffrey E. Hill

Department of Biological Sciences, Auburn University, Auburn, Alabama, USA

Abstract

Song complexity is thought to be a sexually selected trait in passerine birds; however, quantifying relevant parameters of song complexity is the first step in testing the theory that song complexity is a sexually selected trait. We show here that blue grosbeak (*Guiraca caerulea)* males sing a single song type but the properties of that song type vary between renditions. This pattern of song delivery potentially provides females with an opportunity to assess dimensions of song complexity other then repertoire size. Here we characterize song complexity using four measures: (i) element repertoire size, (ii) proportion of distinct song variant, (iii) song versatility, and (iv) syntax consistency. We studied the functional significance of song complexity by comparing measures of song complexity before and after periods of female fertility. We found that male blue grosbeaks sing more song variants, use more versatile arrangements of elements, and maintain more syntax consistency during the fertile period of their social mate than during their social mate's non-fertile period. These results point to a functional relationship between changes in song complexity and periods of female fertility in this species.

Corresponding author: Barbara Ballentine, Duke University, Department of Biological Sciences, P.O. Box 90338, Durham, NC 27702, USA. E-mail: beb5@duke.edu

Introduction

Bird song functions in intra-sexual interactions such as territory establishment and defense, as well as in inter-sexual interactions such as mate attraction (Catchpole and Slater 1995).In both contexts, more complex singing, usually measured in terms of the number of distinct song elements an individual produces, has been shown to be a more effective signal (Andersson 1994). In many species, females have been shown to prefer to mate with males that have larger repertoires (*Acrocephalus paludicola*, Catchpole & Leisler 1996; *Quiscalus quiscula*, Searcy 1992; *Acrocephalus arundinaceus*, Hasselquist et al. 1996; *Ficeducla hypoleuca*, Lampe & Saetre 1995; see Catchpole & Slater 1995 for review). Because a male's

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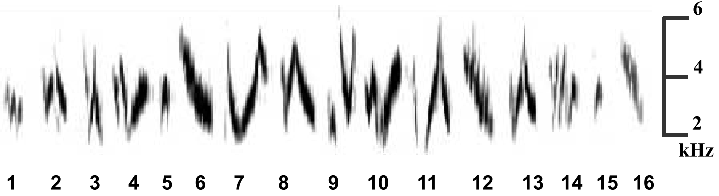
parental ability (Buchanan & Catchpole 2000), condition (Nowicki et al. 2000), genetic quality (Hasselquist 1998), or age (Gil et al. 2001) may correlate with song complexity in avian species, females who prefer to mate with males that have more complex songs or repertoires may gain either direct or indirect benefits. As such, song complexity has potential to function as an indicator mechanism that may be particularly important during female fertile periods.

Song may be directed toward females particularly during their fertile period (Mace 1987), and males often adjust characteristics of song that are associated with male quality, such as song rate, during periods of female fertility (Mace 1987; Cuthill and Macdonald 1990; Part 1991; Slagsvold et al. 1994; Welling et al. 1995; but see Titus et al. 1997). Thus, if males can facultatively adjust the levels of song complexity then they may benefit by minimizing the risk of cuckoldry (Møller 1991), and maximize the probability of obtaining extra-pair fertilizations (Hasselquist et al. 1996) by singing a more complex song during females' fertile period than during their non-fertile period. Little research to date addresses changes in complexity of song as it relates to female fertility (but see Van Horne 1997).

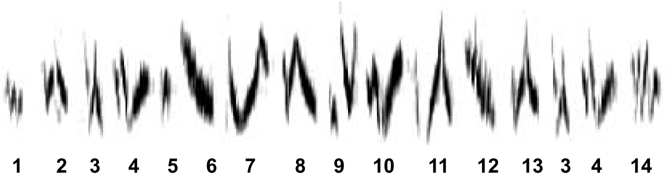
In some species, individual males sing different versions of their species-specific song that are distinct and easily categorized into a repertoire of song types. Other species of birds exhibit yet another level of song complexity in which small variations are introduced into subsequent renditions of the same song type (Podos et al. 1992). Much research has focused on studying the function of song or element repertoires measuring song complexity by counting the number of different songs or elements in an individual's repertoire. However, for many species there may be other relevant features of song complexity, particularly those species that demonstrate both between and within-song-type variation (Podos et al. 1992; Gil and Slater 2000). Studying a species that only exhibits within-song type variation enables us to examine the variation produced in a single song type over the course of the breeding season. Thus, by controlling for between song-type variation, we may gain insight into the significance of within song-type complexity.

We have observed that male blue grosbeaks (*Guiraca caerulea* sing a single song type that they modify to create song variants by rearranging a repertoire of elements (Fig. 1). The purpose of our study was, first, to quantify song complexity in blue grosbeaks, and second, to begin to determine how this song complexity changes with respect to periods of female fertility. We characterized song complexity in blue grosbeaks in four ways: (i) element (or note) repertoire size, (ii) the proportion of distinct song variants used in a bout of singing, (iii) song versatility, and (iv) syntax consistency. Song versatility measures the degree of difference between song variants and is based on the presence or absence of elements in variants. Syntax consistency quantifies the maintenance of certain sequences of elements and is based on the order of elements in variants rather than the presence or absence of elements. Song versatility reflects the ability of a male to produce diverse songs while syntax consistency reflects the ability to maintain certain sequences of elements, which may be important for individual recognition (Weary et al. 1990; Beecher et al. 1994). Our comparison of these

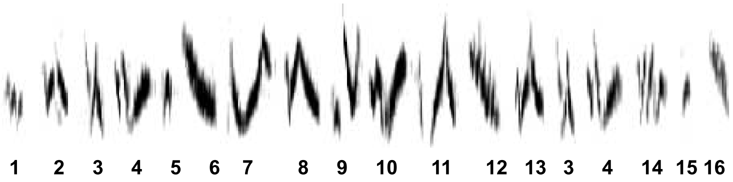
(a) Male 1 element repertoire



(b) Male 1 song variant 1



(c) Male 1 song variant 2



(d) Male 1 song variant 3

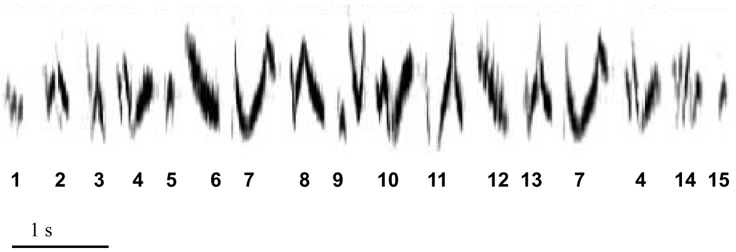


Fig. 1: Sonograms of blue grosbeak song illustrating how songs were annotated. (a) Male 1 has 16 elements in his element repertoire; all of his songs were in some combination of any of these 16 elements. We arbitrarily assigned a number to each element used by males and we annotated all of his songs with these numbers. We repeated this procedure for each male in the population. (b–d) Three song variants are shown for male 1 illustrating the typical ways in which element arrangements varied among song variants for an individual. In some cases, songs vary only in the addition or subtraction of elements (compare b and c). In other cases songs vary in element order as well as addition and subtraction of elements (compare b and c with d)

features of song complexity in relation to periods of female fertility is an initial attempt to test basic hypotheses regarding the function of song complexity. If song complexity functions primarily in sexual signaling, then we predict that males will sing more complex songs during periods of female fertility vs. periods when their social mate is not fertile.

Methods

Data Collection

Data were collected between Apr. and Aug. 1998 at our study site located in Loachapoka, Alabama (82.604°N, 85.593°S). The study site consisted of a complex of agricultural fields planted in either cotton, wheat, or used as pasture and surrounded by secondary growth forest and clear-cut forest (see Keyser and Hill 2000 for more details). We individually marked each adult on the study site with a distinct combination of colored leg bands and an US Fish and Wildlife aluminum band. Male territories were visited daily and all nest locations were determined by following males and females. Once nests were located, they were visually inspected every other day to determine the breeding status of females.

Song recordings were made in the field using a Marantz PMD 222 cassette recorder (Itasca, IL) and a Sennheiser ME-60 directional microphone (Wedemark, Germany), or a Sony cassette recorder with a Sennheiser MHK 70 directional microphone. We recorded subjects during the dawn chorus when all males were singing simultaneously. We followed one individual male from the time it first started singing in the morning (pre-dawn) until its morning bout ended. We considered a bout to have ended if the male stopped singing for a period of at least 2 min. Recordings were made twice for each male, once during the female's fertile period and once during the same female's non-fertile period. Following Birkhead & Moller (1992), we considered pre-nesting, nest building, and egg-laying (until the penultimate egg was laid) to be the females' fertile period and the period after the penultimate egg was laid, incubation, and nestling stages as the non-fertile period.

Data Analysis

Sonograms were generated from digitized versions of recorded songs using SoundEdit 16 software (344 hz frequency resolution, 2.9 ms time resolution) (Macromedia Inc., San Francisco, CA, USA). Sonograms of each recording for each male were annotated into a sequence of elements. Elements are the smallest independent units produced by each male separated by periods of silence greater then 50 ms and are typically made up of single notes (Fig. 1). When two notes always appeared together throughout a male's song bout and were separated by periods of silence of less then 30 ms, two notes were considered a single element (see elements 9 and 11 in Fig. 1). A song is a string of elements grouped together, and songs are separated from each other by a period of silence of approximately 8 s. Using this definition, we found that elements were shared among individuals, whereas the order of element arrangements was not necessarily shared.

Element Repertoire Size

Song element repertoires were determined by visual inspection of sonograms. A number was assigned to each novel element in a song and a catalog of elements was assembled for each male. An independent observer verified element categories. We determined element repertoires for each individual by counting novel elements as they appeared. We considered element repertoires to be complete by using an exhaustion curve of the number of new elements detected as a function of number of songs inspected (Kroodsma 1982) (Fig. 2). We had good song recordings for the dawn chorus of 17 territorial males. We observed that for these 17 males, the element repertoire was complete after a maximum of 17 songs. As we had at least 20 songs recorded for all 17 males, we included all 17 males in our analysis. However, for various reasons we only had good recordings for both fertile and non-fertile periods for 14 of the 17 males.

Proportion of Distinct Song Variants

Each song was annotated, using the numbers that were assigned to each novel element, into a sequence of numbers (Fig. 1). All songs from a song bout were sorted by element sequence to identify all song variants. Songs that were considered the same song variant each contained the exact order of all elements. We calculated the proportion of distinct song variants (P_{sv}) as $P_{sv} = N_{sv}/N_t$, where N_{sv} is the number of distinct song variants observed and N_t is the total number of songs recorded. There was no relationship between the number of songs recorded and the proportion of variants observed in all song bouts recorded ($r = -0.18$, $p = 0.29$, $n = 36$). Distinct song variants subsequently were used to calculate song versatility and syntax consistency indices, as described next.

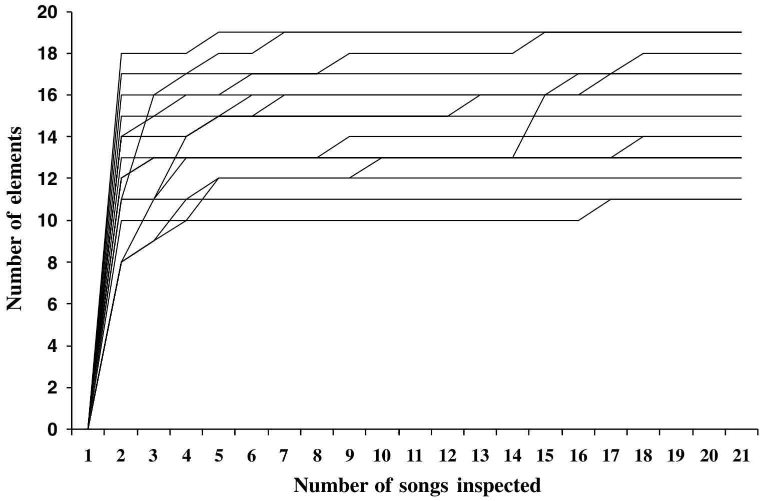


Fig. 2: Plot of the exhaustion curves of new elements against total elements for 17 males recorded in our study

Table 1: Example of matrix data taken from figure 1 to calculate versatility

Element	Song variant 1	Song variant 2	Song variant 3
1	1	1	1
2	1	1	1
3	1	1	1
4	1	1	1
5	1	1	1
6	1	1	1
7	1	1	1
8	1	1	1
9	1	1	1
10	1	1	1
12	1	1	1
13	1	1	1
14	1	1	1
15	0	1	1
16	0	1	0

Song Versatility

Song versatility was estimated in three steps. First, for each male we coded all distinct song variants observed based on the presence or absence of elements in each sequence such that each distinct variant was now represented by a series of 1s and 0s (Table 1). Secondly, we calculated all possible pairwise Jaccard's coefficients of similarities (Sokal & Rohlf 1981) between song variants for each male (after Podos et al. 1992). The coefficient of similarity varies from 0 to 1, and was calculated as $(CC_j)_{a,b} = c/(c + u_a + u_b)$ where a and b are the song variants being compared, c is the number of elements common to both a and b, u_a is the number of elements unique to a, and u_b is the number of elements unique to b. Finally, we extracted the first principal component of the matrix of Jaccard's coefficients of similarities for all pairwise comparisons of song variants for each male and calculated the proportion of the total variance in Jaccard's matrix accounted for by the eigenvalue of the first principal component. Higher values of the first principal component reflect greater similarity among individual coefficients of each song variant. Thus, we subtracted the proportion of the variance associated with the first principal component from 1.00 to obtain a measure of song versatility.

Syntax Consistency

To estimate syntax (i.e. sequential) consistency of song elements, each song element was assigned a unique number and songs were coded using numbers to identify each element and the element's relative position within a song (Table 2). We constructed a correlation matrix to calculate correlations between all variants based on position of elements within each variant (Table 2). We then evaluated variation in sequential placement of all elements across all songs sung by an

Table 2: Example of matrix data taken from figure 1 to calculate syntax consistency

	Position of Element																		
Song varaints	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	3a	4a	7a
SV1	1	2	3	4	5	6	7	8	9	10	11	12	13	16	0	0	14	15	0
SV2	1	2	3	4	5	6	7	8	9	10	11	12	13	16	17	18	14	15	0
SV3	1	2	3	4	5	6	7	8	9	10	11	12	13	16	17	0	0	15	14

[a] Denotes the second appearance of an element in a song.

individual. Our measure of syntax consistency was the proportion of the total variance accounted for by the first eigenvalue of the element placement correlation matrix of each male (Sokal & Rohlf 1981).

We only had recordings during both fertile and non-fertile periods for 14 of 17 males. Of those 14 males for which we could compare sonograms, there were cases in which we were unable to obtain song rate data for both the fertile and non-fertile periods because a male sang inconsistently or because dawn chorus length data did not have an accurate start or stop time. We used a paired t-test to examine significance of changes in our measures of complexity (element repertoire, song variants, versatility and syntax consistency) for songs sung during different periods of the female fertile cycle, as well as for differences in song rate and the length of the dawn chorus. Because these analyses reflect a paired design, we can only include those males for which we have reliable data for both fertile and non-fertile periods.

Results

We recorded at least one song bout for each of the 17 males; the number of song variants we observed per male ranged from five to 138 variants. Not all males were recorded during both their females' fertile period and non-fertile period. Of those males for which we had data both for fertile and non-fertile periods, males sang significantly longer dawn choruses ($\bar{x} = 40.2 \pm 15.4$ min, $\bar{x} = 27.5 \pm 15.8$ min, respectively) ($t = 1.88$, $p = 0.05$, $n = 10$) and at significantly higher song rates during their female's fertile period than during the non-fertile period ($\bar{x} = 5.9 \pm 0.9$ songs/min, $\bar{x} = 5.4 \pm 0.6$ songs/min, respectively) ($t = 2.16$, $p = 0.03$. $n = 11$).

Element repertoire size did not differ between females' fertile and non-fertile periods ($t = 0.62$, $p = 0.55$, $n = 14$) (Fig. 3a). Males sang significantly more song variants ($t = 2.60$, $p = 0.02$, $n = 14$) (Fig. 3b) during females' fertile periods than during females' non-fertile periods. Song variants were significantly more versatile ($t = 7.55$, $p = 0.0001$, $n = 14$) (Fig. 3c) and sung with significantly more syntax consistency ($t = 5.23$, $p = 0.0002$, $n = 14$) (Fig. 3d) during females' fertile periods than during females' non-fertile periods. Element repertoire was correlated with the proportion of distinct song variants ($r = 0.640$, $p = 0.03$, $n = 17$) and with versatility ($r = 0.671$, $p = 0.02$, $n = 17$), but not with syntax consistency

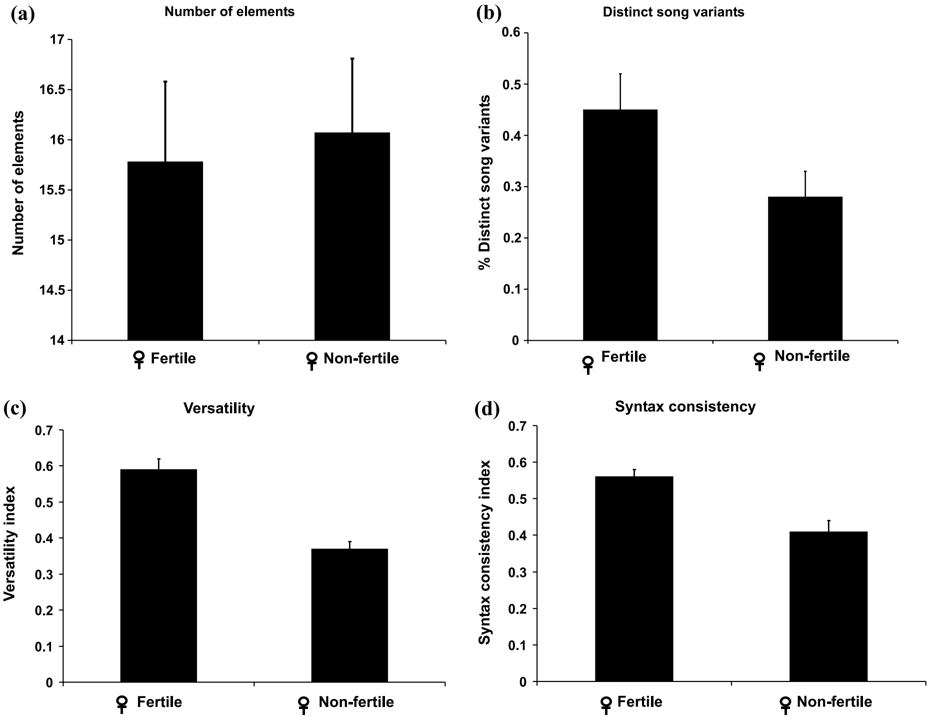


Fig. 3: Properties of male song during females' fertile and non-fertile periods. Error bars represent standard error. (a) Number of elements in males' repertoires, (b) Percent distinct song variants among recorded songs, (c) Song versatility, and (d) Syntax consistency for each period

(r = −0.367, p = 0.9, n = 17). Probabilities reported for the above correlations reflect the Bonferroni correction for multiple comparisons. For males who sang during their females' fertile period, the variation between males for our measures of song complexity was as follows: element repertoire size CV = 0.182, n = 17; proportion of distinct song elements CV = 0.502, n = 17; song versatility CV = 0.301, n = 17, syntax consistency CV = 0.187, n = 17.

Discussion

The primary goals of this study were to quantify song complexity in a species that exhibits only within-song-type variation, and to begin to understand the function of within-song-type complexity by correlating changes in vocal complexity to periods of female fertility. We found that male blue grosbeaks did not vary in the number of element types expressed between their females' fertile and non-fertile periods. Thus, had we used this conventional measure of vocal complexity, we would have found no relationship between vocal complexity and female fertility status. However, when we looked at higher orders of vocal complexity (proportion of distinct song variants, song versatility, and syntax consistency) we found that males exhibit different levels of complexity that correspond to their females' reproductive cycle. Not only do males sing more distinct song variants during their females' fertile period but they also sing with increased song versatility. That is, blue grosbeaks use their element repertoire to create a more complex repertoire of song variants during the females' fertile period than during the non-fertile period. We also found that syntax consistency changed with respect to female fertility such that during female fertile periods, males conserved certain sequences of elements with more tenacity than during the non-fertile period. Apparently, blue grosbeaks have a fixed repertoire of elements with which they create song variants. It is the manner in which they combine and arrange these elements that changes with respect to female fertility. Thus, it is likely that song complexity expressed as within-song-type variation (measured by proportion of distinct song variants and song versatility) and syntax consistency have functional significance in blue grosbeaks.

Why might female blue grosbeaks assess males according to their song complexity? One possibility is that within-songtype complexity, like between-song-type complexity, indicates important aspects of male quality. It has been shown that variation in between-song complexity, in terms of repertoire size, correlates with measures of male quality such as condition during development (Nowicki et al. 2000; 2002), parental ability (Buchanan & Catchpole 2000), and age (Gil et al. 2001), and, may communicate therefore, information to conspecifics about male quality that it is used as a criterion in female choice (see Catchpole & Slater 1995 for review). Given that between-song complexity, as measured by song repertoire size, may function as an indicator mechanism, it seems reasonable to propose that within-song-type variation similarly signals male quality. Indeed, as might be expected from a potential indicator trait, we observed a substantial amount of variation between males in the expression of vocal complexity. However, the function of within-song-type variation is less understood than the function of between-song complexity. Males perceive within-song-type variation (Stoddard et al. 1988) and are able to categorize variants (Stoddard et al. 1992). However, in playback experiments, male song sparrows (*Melospiza melodia*) showed a greater response to between-song-type variation than within-song-type variation (Searcy et al. 1995), but when responding to a simulated intrusion, males would use more song variants suggesting that within-song-type variation may somehow function in interactions with other males (Searcy et al. 2000). Male bobolinks (*Dolichonyx oryzivorus*) use more song variants when presented with caged females than when presented with caged males suggesting that perhaps within-song-type variation may function in male–female interactions (Ammer & Capp 1999).

Although we do not have direct evidence of the sexual function of within-songtype variation, our data are consistent with the idea that within-song-type variation functions in sexual contexts. Element repertoire is correlated with the proportion of distinct song variants and song versatility and perhaps by performing more song variants with more versatility, blue grosbeaks are able to enhance the perceptual complexity of their element repertoire. While vocal complexity in terms of within-song-type variation and versatility may function as signals, our data also suggest that maintaining the relative sequences of elements may also serve a function. We found that syntax consistency, which is the manner in which a sequence of elements appears in a song, correlates to changes in female fertility. Syntax consistency may provide information to females regarding male identity (Weary et al. 1990) that may be important when females are evaluating prospective mates in a group of signaling males. Female passerines have been shown to discriminate among individuals in their neighborhood based on song and to recognize their mate's song (Erwin 1994; O'Loghelen & Beecher 1999). Thus, maintaining certain sequences of elements may facilitate individual recognition and may be particularly critical during female fertile periods. At the same time, being as showy as possible in terms of element repertoire delivery may be particularly important during female fertile periods.

Along with changes in song complexity, we also found that blue grosbeaks sing longer dawn choruses and sing with increased song rates during the dawn chorus of their females' fertile period than during their females' non-fertile periods. Our data on song rate and bout length during the dawn chorus corroborates the findings of most other studies (Mace 1987; Cuthill & Macdonald 1990; Slagsvold et al. 1994; Welling et al. 1995; but see Part 1991). This pronounced peak of singing activity during female fertile periods may also function as an assessment signal (Otter et al. 1997). Thus, it is likely that song rate and bout length during dawn chorus in blue grosbeaks, as in other species, functions as an assessment signal.

More studies are necessary to identify the function of within-song-type complexity in blue grosbeaks as well as in other species (Searcy & Nowicki 1999). It is likely that other passerine species with indeterminate repertoire sizes (e.g. *Vireo olivaceus*, *Piranga rubra* and *Piranga olivacea*) may actually exhibit a considerable degree of within-song-type variation. A quantitative study of song in such species would identify the degree to which they do or do not use within-song-type variation. Also, our data suggest that experimental studies using blue grosbeaks may elucidate the function of within-song-type complexity. We know of no studies that demonstrate whether females are sensitive to within-song-type variation. Future studies with blue grosbeaks should include experiments that test whether females are in fact sensitive to within-song-type complexity. Finally, because blue grosbeaks only exhibit within-song-type variation, they may be ideal subjects for studying the development of within-song-type variation (e.g. Nowicki et al. 1999).

Acknowledgements

We especially thank Amber Keyser for help recording males. We thank Mary Mendonça for lending us recording equipment. We thank our field crew including Lynn Siefferman, Johathan Arail, Renée Duckworth, Joe Smith, Scott Lovell, Angela Martin and Kelly Volansky. This manuscript was much improved by Lynn Siefferman, Anne Dervan, Jeremy Hyman, Steve Nowicki and two anonymous reviewers. We especially thank Anne Dervan for her help with developing protocols for annotation of songs. We thank Pamela Holloway for her help with data entry. We also thank Susan

Peters for verifying song element categories. This research was supported by the Department of Biological Sciences at Auburn University, the Alabama Agricultural Experiment Station, and American Cyanamid Company, Global Agricultural Products Division.

Literature Cited

Ammer, F. K. & Capp, M. S. 1999: Song versatility and social context in the bobolink. The Condor **101,** 686.

Andersson, M. B. 1994: Sexual Selection. Princeton University Press, Princeton, NJ.

Beecher, M. D., Campell, S. E. & Burt, J. M. 1994: Song perception in the song sparrow: birds classify by song type but not by singer. Anim. Behav. **47,** 1343—1351.

Birkhead, T. R. & Moller, A. P. 1992: Sperm Competition in Birds: Evolutionary Causes and Consequences. Academic Press, London.

Buchanan, K. L. & Catchpole, C. K. 2000: Song as an indicator of male parental effort in the sedge warbler. Proc. R. Soc. Lond. B **267,** 321—326.

Catchpole, C. K. & Leisler, B. 1996: Female aquatic warbler (*Acrocephalus paludicola)* are attracted by playback of longer and more complicated songs. Behaviour **133,** 1153—1164.

Catchpole, C. K. & Slater, P. J. B. 1995: Bird Song. University Press, Cambridge.

Cuthill, I. C. & Macdonald, W. A. 1990: Experimental manipulation of the dawn and dusk chorus in the blackbird, *Turdus merula*. Behav. Ecol. Sociobiol. **26,** 209—216.

Erwin, N. 1994: Individual recognition of song by the female song activity of the male in the reed bunting. J. Orn. **132,** 217—222.

Gil, D. & Slater, P. J. B. 2000: Song organisation and singing patterns of the willow warbler, *Phylloscopus trochilus*. Behavior **137,** 759—782.

Gil, D., Cobb, J. L. S. & Slater, P. J. B. 2001: Song characteristics are age dependent in the willow warbler, *Phylloscopus trochilus*. Anim. Behav. **62,** 689—694.

Hasselquist, D. 1998: Polygyny in great reed warblers: a long-term study of factors contributing to male fitness. Ecology **79,** 2376—2390.

Hasselquist, D., Bensch, S. & Schantz, T. V. 1996: Correlation between male song repertoire, extra pair paternity and offspring survival in the great reed warbler. Nature **381,** 229—232.

Keyser, A. J. & Hill, G. E. 2000: Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. Behav. Ecol. **11,** 202—209.

Kroodsma, D. E. 1982: Song repertoires: problems in their definition and use. In: Kroodsma, D. E. & Miller, E. H. (eds): Acoustic Communication in Birds. Academic Press, New York.

Lampe, H. M. & Saetre, G.-P. 1995: Female pied flycatchers prefer males with larger song repertoires. Proc. R. Soc. Lond. B **262,** 163—167.

Mace, R. 1987: The dawn chorus in the great tit *Parus major* is directly related to female fertility. Nature (Lond.) **330,** 745—746.

Møller, A. P. 1991: Why mated songbirds sing so much: mate guarding and male announcement of mate fertility status. Am. Nat. **138,** 994—1014.

Nowicki, S., Peters, S., Searcy, W. A. & Clayton, C. 1999: The development of within-song type variation in song sparrows. Anim. Behav. **57,** 1257—1264.

Nowicki, S., Hasselquist, D., Bensch, S. & Peters, S. 2000: Nestling growth and song repertoire size in great reed warblers: evidence for song learning as an indicator mechanism in mate choice. Proc. R. Soc. Lond. B **267,** 2419—2424.

Nowicki, S., Searcy, W. A. & Peters, S., Brain development, song-learning and mate choice in birds: a review and experimental test of the 'nutritional stress hypothesis'. (In press).

O'Loghelen, A. L. & Beecher, M. D. 1999: Mate, neighbour and stranger songs: a female song sparrow perspective. Anim. Behav. **58,** 13—20.

Otter, K., Chruszcz, B. & Ratcliffe, L. 1997: Honest advertisement and song output during the dawn chorus of black-capped chickadees. Behav. Ecol. **8,** 167—173.

Part, T. 1991: Is dawn singing related to paternity insurance? The case of the collared flycatcher. Anim. Behav. **41,** 451—456.

Podos, J., Peters, S., Rudnicky, T., Marler, P. & Nowicki, S. 1992: The organization of song repertoires in song sparrows: themes and variations. Ethology **90,** 89—106.

Searcy, W. A. 1992: Song repertoire and mate choice in birds. Am. Zool. **32,** 71—80.

Searcy, W. A. & Nowicki, S. 1999: Functions of song variation in song sparrows. In: The Design of Animal Communication (Hauser, M. D. & Konishi, M., eds). The MIT Press, Cambridge, pp. 319—342.

Searcy, W. A., Podos, J., Peters, S. & Nowick, S. 1995: Discrimination of song types and variants in song sparrows. Anim. Behav. **49,** 1219—1226.

Searcy, W. A., Nowicki, S. & Hogan, C. 2000: Song type varaints and aggressive context. Behav. Ecol. Sociobiol. **48,** 358—363.

Slagsvold, T., Dale, S. & Saetre, G. P. 1994: Dawn singing in the great tit (Parus major): mate attraction, mate guarding, or territorial defence? Behaviour **131,** 115—138.

Sokal, R. R. & Rohlf, F. J. 1981: Biometry, 2nd edn. W.H. Freeman & Co, San Francisco.

Stoddard, P. K., Beecher, M. D. & Willis, M. S. 1988: Response of territorial male song sparrows to song types and variations. Behav. Ecol. Sociobiol. **22,** 125—130.

Stoddard, P. K., Beecher, M. D., Loesche, P. & Campbell, S. E. 1992: Memory does not constrain individual recognition in a bird with song repertoires. Behaviour **122,** 247—287.

Titus, R. C., Chandler, C. R., Ketterson, E. D. & Nolan Jr, V. 1997: Song rates of dark-eyed juncos do not increase when females are fertile. Behav. Ecol. Sociobiol. **41,** 165—169.

Van Horne, B. 1997: Assessing vocal variety in the winter wren, a bird with a complex repertoire. The Condor **97,** 39—49.

Weary, D. M., Norris, K. J. & Falls, J. B. 1990: Song features birds use to identify individuals. The Auk **107,** 623—625.

Welling, P., Koivula, K. & Lahti, K. 1995: The dawn chorus is linked with female fertility in the Willow Tit '*Parus montanus*'. J. Avi. Biol. **26,** 241—246.

Received: March 20, 2002

Initial acceptance: May 8, 2002

Final acceptance: September 12, 2002 (S. K. Sakaluk)