sound presented contralaterally to the dominant hemisphere tends to be perceived first. See also D. Kimura [*Can. J. Psychol.* **15**, 166 (1961)].

17. The number of correct identifications of stimuli presented to the right (R) and left (L) ears are entered into the formula $(R - L)/(R + L) \times 100$, as described by M. Studdert-Kennedy and D. Shankweiler [*J. Acoust. Soc. Am.* **48**, 579 (1970)].

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Reproductive Development in a Female Songbird: Differential Stimulation by Quality of Male Song

Abstract. *Female canaries exposed to playback of large repertoires of male songs built nests faster and laid more eggs than did those females exposed to smaller song repertoires: females are attentive to attributes of male song, and their choices have played a role in the evolution of oscine singing behaviors.*

The vocalizations of male birds, in addition to repelling other territorial males, attract and stimulate mates. Darwin (*1*) championed the "melody of voice" as functioning in the "charming of females," and enhancement of female reproductive development by male sounds has subsequently been demonstrated (*2*). With females exerting the choice in mate selection (*3*), female discrimination is implicated as a significant selective force in the evolution of the bewildering diversity of male singing behaviors that exist among the songbirds. I now report that female reproductive behavior is differentially stimulated by variations in the complexity of intraspecific song.

The experimental subjects were selected from an inbred strain of Belgian "Wasserschlager" canaries (*Serinus canarius*). In these birds, a typical male song repertoire consists of 30 to 40 distinct note patterns or syllables. Four 10-minute experimental tapes were prepared by selective editing of a large number of recordings of natural canary song. Two tapes had large song repertoires of approximately 35 syllable types, and two had small song repertoires of only five syllable types (*4*). For the two with large repertoires, 15 songs averaging 30 seconds in length were selected from tapes of each of two normal males. For each of the tapes with smaller song repertoires, songs of a normal male were searched for five naturally occurring sequences of five different syllable types (for example, ABCDE), chosen because of their relatively high frequency of occurrence in the songs; these sequences were edited and spliced together in random order to make 15 different 30-second songs. Because of inequalities in total song lengths in the different categories, a final editing of tapes yielded, in the two small-repertoire tapes, 14 songs totaling 450 seconds and 15 songs totaling 441 seconds, and in the two large-repertoire tapes, 14 songs totaling 439 seconds and 15 songs totaling 447 seconds. The 14 or 15 songs for each experimental tape were then spliced together, with 10 seconds between songs, to form singing bouts.

During September and October 1974, 24 virgin female canaries were selected for uniformity of age (6 to 7 months) and gonadal development (the largest follicle size was ≤ 0.4 mm). On 17 December four treatment groups were established, with siblings distributed among the groups. The six birds in each group were paired randomly. Each pair was housed in a metal canary cage (27 by 28 by 52 cm); a partition divided the cage between the two birds and allowed auditory but not visual contact. Each of the 12 cages was placed in a sound attenuation chamber (IAC model AC-1) equipped with loudspeakers. To prevent the birds from looking at themselves (*5*), the reflective interior window of each chamber was covered. Day lengths prior to 17 December were natural, but during the experimental period, the light : dark cycle was constant (9.5 : 14.5).

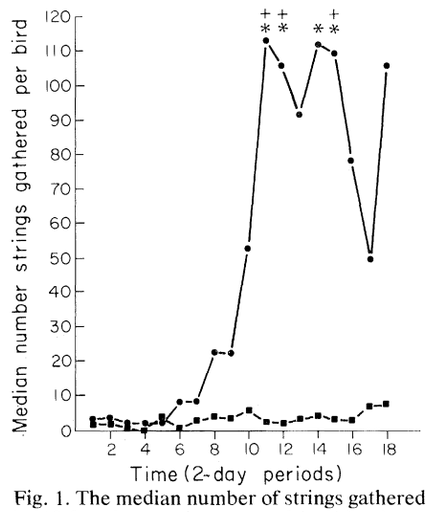

Fig. 1. The median number of strings gathered by 12 female canaries exposed to either large (●) or small (■) male song repertoires. There were significant differences between the two groups during period 11, 12, 14, and 15 (Mann-Whitney U test; *; $P < .05$; *+, $P < .025$).

At 1200 hours on 21 January 1975 (day 1 of the experiment), each bird was supplied with a metal-wire nest cup and a bundle of 75 10-cm strings attached to the side of the cage. Each day at 1200 hours, all eggs that were laid and all strings that were pulled from the bundle and left on the cage floor or placed in the nest cup were removed and counted; the string bundle was then replenished to 75 strings. Gathering of strings from a dispenser is a sensitive assay of reproductive development, for, in photoperiodically induced reproductive development in female canaries, string gathering is highly correlated with the diameter of the largest ovarian follicles and with oviduct weight, and the latter is highly correlated with plasma levels of luteinizing hormone (*6*).

Even though recorded songs had not yet been played on day 6, three females were building feverishly (*7*), and one female laid an egg. A fourth female began gathering all 75 strings on day 7. Beginning at 1200 hours on day 7 and continuing through day 36, the females were exposed to the 10-minute male song bouts 12 times during 3-hour periods in the morning and in the afternoon. The group including the female that laid an egg on day 6 was intentionally placed in the small song repertoire group (*8*). Subjects for the other three treatment groups were selected at random.

String-gathering scores were tabulated for 36 days, 6 preceding and 30 during exposure to songs. Individual string-gathering scores were summed over successive 2-day periods. By days 21 to 22 (period 11) the median number of strings pulled by the 12 female canaries exposed to the larger song repertoires significantly exceeded the number pulled by the 12 canaries exposed to the small song repertoires (Fig. 1). Even if the three or four birds exhibiting high string-gathering scores prior to their exposure to the song stimuli are culled from the experiment, the difference between the groups remains statistically significant (*9*). Correlated with the high levels of string gathering were higher levels of egg laying. By day 36 of the experiment, five females exposed to the larger song repertoires had laid 15 eggs, while two birds exposed to the smaller song repertoires had laid only five eggs; monitoring of eggs (but not

nest building) continued through day 54, by which time the egg ratio had reached 28 to 10 (large repertoire, five birds to small repertoire, three birds). Thus, females exposed to male song with a larger number of syllable types were stimulated into reproductive condition faster than were those females exposed to male song with a smaller number of syllable types. The rate at which eggs are laid (and thus offspring produced) is a significant component of fitness, and the sooner the males can attract and stimulate females into reproductive condition, the higher will be their relative fitness.

There are several interpretations for the mechanism involved in this female response to the quality of male song.

1) Both males and females of many songbird species learn and are capable of singing the details of songs heard during a sensitive period early in life. Whether females sing these learned songs naturally (*10*) or, as in most species, only after testosterone therapy (*11*), the female generally sings the "native dialect" (*12*). Males generally respond strongest to songs most like their own, that is, songs of their own dialect (*13*); it is conceivable that females will also be most stimulated by (and therefore may select) a mate whose songs most closely match her own song or song template (*14*). In this experiment, it was more probable that song components learned by females would be matched by the large than by the small repertoire of male songs. This would result in greater stimulation of the females exposed to the 35 rather than to the five syllable types. Mate selection and stimulation based on vocal signals common to the two sexes is highly possible (*14*) and could [together with possible sexual differences in dispersal times and distances (*15*) and possible sexual differences in the relative timing of the sensitive period for song learning] play a crucial role in the population biology of many species.

2) A greater diversity of male song stimuli could reduce habituation and maximize stimulation during male-female interactions. Female stimulation and gonadal development might then be achieved in proportion to the size of the male song repertoire, which could, in turn, be an index of the overall vigor of a male. Male Bewick's wrens (*Thryomanes bewickii*) hatched late in the breeding season develop smaller song repertoires than do those hatched earlier (*16*). In general, birds hatched later have a poorer chance of surviving (*17*); song repertoire size could then be an index of the date of hatching as well as a male's potential survival and vigor. By chance alone, the larger the repertoire of song components, the larger will be the number of components that are shared with the early experiences of potential mates —the size of the repertoire and the degree of matching could interact in a manner to stimulate females maximally.

3) A third possibility is that not all components of a male's song serve the same function, and that the females hearing the larger repertoires were exposed to the "mate stimulation song components," whereas by chance the tapes of the smaller song repertoires lacked those components. No data are available, but the literature for some wood warblers (Parulidae) suggests this possibility (*18*).

Whatever the mechanism involved, female canaries are attentive to the quality of male advertising signals. The highly "skilled salesmanship among the males" has led to an "equally well-developed sales resistance and discrimination among the females" (*19*). Epigamic selection has played a key role in orchestrating the diversity of male singing behaviors.

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References and Notes

1. C. Darwin, *The Descent of Man and Selection in Relation to Sex* (Merrill and Baker, New York, 1874), p. 367.
2. In ringdoves (*Streptopelia risoria*) and budgerigars (*Melopsittacus undulatus*) [B. F. Brockway, *Anim. Behav.* **13**, 575 (1965); in *Bird Vocalizations*, R. A. Hinde, Ed. (Cambridge Univ. Press, Cambridge, 1969), pp. 131–158; R. W. Ficken, A. van Tienhoven, M. S. Ficken, F. C. Sibley, *Anim. Behav.* **8**, 104 (1960); D. S. Lehrman and M. Friedman, *ibid.* **17**, 494 (1969); F. Nottebohm and M. E. Nottebohm, *ibid.* **19**, 313 (1971).
3. For example, see G. Orians, *Am. Nat.* **103**, 589 (1969).
4. A repertoire size of five syllable types is within the range of that developed by experimental birds of P. Marler, M. Konishi, A. Lutjen, and M. S. Waser [*Proc. Natl. Acad. Sci. U.S.A.* **70**, 1393 (1973)].
5. D. F. Lott and P. N. Brody, *J. Comp. Physiol. Psychol.* **62**, 311 (1966).
6. B. F. Follett, R. A. Hinde, E. Steel, T. J. Nicholls, *J. Endocrinol.* **59**, 151 (1973).
7. All available 75 strings were placed in the nest-cup on two to five of the 6 days, and all 75 strings were gathered (sum of strings in nest and on cage floor) on four to six of those days.
8. The group with the physiologically most advanced female was given the auditory stimuli presumed to be less stimulative; in order to yield significantly greater stimulation by the richer sound stimuli, the gonadal development of the 12 birds played the larger song repertoires would then have to catch and surpass that of the 12 played the smaller song repertoires.
9. If those four females gathering 75 strings on at least one of the first 7 days of the experiment are eliminated from the calculations, precisely the same pattern of significance is seen ($N = 10$ females in each group); if only those three females gathering 75 strings on at least 1 day during the first 6 days of the experiment are culled, the groups still differ significantly during periods 11, 12, and 16 ($P < .05$; $N = 10$ for birds exposed to large song repertoires, $N = 11$ for birds exposed to small song repertoires).
10. For example, see R. E. Lemon, *Behaviour* **32**, 158 (1968).
11. M. Konishi, *Z. Tierpsychol.* **22**, 770 (1965); review in M. D. Kern and J. R. King, *Condor* **74**, 204 (1972).
12. Some degree of vocal learning, together with relatively limited dispersal from the locality at which males learn songs, results in the phenomenon of neighboring individuals possessing vocalizations more like one another than like birds breeding at any other location. This sharing of learned songs by neighboring individuals has been called "dialects."
13. B. Bertram, *Anim. Behav. Monogr.* **3**, 79 (1970); M. A. Harris and R. E. Lemon, *Condor* **76**, 33 (1974); R. A. Hinde, *Anim. Behav.* **6**, 211 (1958); M. Kreutzer, *Rev. Comp. Anim.* **8**, 287 (1974); R. E. Lemon, *Anim. Behav.* **15**, 538 (1967); *Behaviour* **32**, 158 (1974); M. M. Milligan and J. Verner, *Condor* **73**, 208 (1971); G. Thielcke and K. Linsenmair, *J. Ornithol.* **104**, 372 (1963).
14. P. Marler and M. Tamura, *Science* **146**, 1483 (1964); F. Nottebohm, *Condor* **71**, 299 (1969).
15. A. A. Dhondt and J. Huble, *Bird Study* **15**, 127 (1968); S. C. Kendeigh, *Ill. Biol. Monogr.* **18**, 1 (1941); F. S. Tompa, *Acta Zool. Fenn.* **109**, 1 (1964); J. Verner, *Bird-Banding* **42**, 92 (1971).
16. D. E. Kroodsma, thesis, Oregon State University (1972).
17. M. P. Harris, *Ibis* **108**, 17 (19 → D. N. Nettleship, *Ecol. Monogr.* **42**, 239 (1972); C. M. Perrins, *Ibis* **108**, 132 (1966).
18. D. H. Morse, *Nature (London)* **226**, 659 (1970); compare with M. R. Lein, *ibid.* **237**, 48 (1972).
19. G. C. Williams, *Adaptation and Natural Selection* (Princeton Univ. Press, Princeton, N.J., 1966), p. 186.

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