important since the male's sperm is very likely to fertilize almost all of the mature eggs that the female lays after mating (*16*). Among the variables that contribute to the variation in female weight, an important one is the large amount of fat noted in the abdomens of heavy females. A female with large fat reserves would be a good mate choice since she has demonstrated abilities to store resources in a situation where there is intense competition for food (*17*).

The tettigoniids are an ideal group in which to examine differences in sex roles within a discrete taxon. Neither sex of any species is known to exhibit care of offspring. Interspecific variation in female egg investment does not appear to vary as much as male contribution to spermatophores. Male weight loss per spermatophore ranges from 2 to 3 percent in some species (*18*) to 30 percent in others (*19*). There should, therefore, be differences in the behavior of the sexes of species with low male investment and those with high male investment. Studies of the reproductive behavior of katydids indicate that males of many species vigorously compete. Males of the genus *Orchelimum* space themselves acoustically and often fight for the best singing perches, that is, perches likely to have females nearby (*20, 21*). Females in the field often take several hours to select a mate (*21*). Male *Orchelimum* invest about 10 percent of body weight (*21*). *Copiphora rhinoceros*, a neotropical species, has a very large spermatophore; males of this species prolong courtship by repeatedly withdrawing from the female (*22*). Mormon crickets lose an average of 20 percent of their body weight. In this species, spermatophores are likely to be a limiting resource for female reproduction. Since food, especially protein sources, is vigorously contested by both sexes in the band (*17*), spermatophore nutrients may be very important to female reproduction. A behavioral sex role reversal with female competition and male mate discrimination results.

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9. Although male prezygotic nutrient investments have been described as parental effort (*8*), it has been argued that these investments are mating effort because they are used to acquire mates (*2*). They are, however, a kind of mating effort that benefits the female's reproduction and reduces the male's maximum number of fertilizations. As a result, they should influence the evolution of sexual differences in a way similar to true parental investment such as parental care [D. T. Gwynne, in *Sperm Competition and the Evolution of Animal Mating Systems*, R. L. Smith, Ed. (Academic Press, New York, in press)].
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11. Spermatophore proteins are known to be important to female reproduction. Labeled spermatophore proteins are incorporated into the ovaries of grasshoppers [T. Friedel and C. Gillott, *J. Insect Physiol.* **23**, 145 (1977)] and butterflies [C. L. Boggs and L. E. Gilbert, *Science* **206**, 83 (1979)]. Research with my co-workers has shown that labeled amino acids from katydid spermatophores are used in both eggs and somatic tissues. Spermatophore and glandular feeding by female tree crickets increases the number of eggs they lay [P. Bell, thesis, University of Toronto (1979)].
12. The study was conducted about 12 km southeast of Greystone, Colo., in a high plains sagebrush area during July 1980.
13. Mormon crickets commonly reach pest status in the western United States, where they move in large feeding bands [F. T. Cowan, *U.S. Dep. Agric. Tech. Bull. 161* (1929); C. Wakeland, *U.S. Dep. Agric. Tech. Bull. 1202* (1959)].
14. Several females that had fresh spermatophores but were not observed mating were included in the sample. All specimens were frozen and later weighed, measured, and dissected. Spermatophores were removed before weighing.
15. There were no statistically significant differences in the average sizes (head widths and pronotum lengths) of rejected and mated females. The average ovary weight and number of mature eggs of mated females were larger than those of rejected females. These differences were not significant, however, probably because sample sizes were not large enough (Mann-Whitney *U* tests). No observable differences in the ages of mated and rejected females were noted. Both groups were over 10- to-12-day-old adults as judged by the techniques described by A. C. Neville [*Oikos* **14**, 1 (1963)].
16. In *Anabrus*, oviposition follows a mating [N. Criddle, *Can. Entomol.* **58**, 261 (1926)]. G. A. Parker [*Biol. Rev. Cambridge Philos. Soc.* **45**, 525 (1970)] has reported that the last male to mate in most insects obtains a higher proportion of egg fertilizations. D. T. Gwynne (*9*) has shown that the sperm of the last male usually has precedence in groups where males invest nutrients, parental care, and so forth [see also R. L. Smith, *Science* **205**, 1029 (1979)].
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Sparrows Learn Adult Song and More from Memory

Abstract. *Male swamp sparrows reared in the laboratory and exposed to taped songs during infancy produce accurate imitations of the material following an 8-month interval with no rehearsal. When the first rehearsal occurs, at about 300 days of age, large numbers of syllables are perfected. They are developed through invention and improvisation as well as imitation. Most are discarded at the time of song crystallization. Hence, these songbirds learn more than they manifest in full adult song.*

Many and perhaps all songbirds acquire the normal song of their species through learning (*1*). Some songbirds retain an ability to develop new songs throughout life (*2*). Others lose this ability early, so that songs developed at sexual maturity remain virtually unchanged over subsequent breeding seasons. Sensitive periods for vocal learning are commonly found; laboratory-reared birds of several species learn from taped songs played to them in infancy more readily than later in life (*3*). In some this occurs even though full song does not commence until late adolescence or adulthood. Thus certain songbirds may be said to display a remarkable capacity to learn to sing from memory. There is an early perceptual phase of listening to others and learning from them and a later phase of sensorimotor development in which birds monitor their own voice in perfecting song production.

In the sensorimotor phase, song does not spring forth fully formed, but is prefaced by a period of subsong (*4*). In some species subsong begins in infancy, and can follow soon after the perceptual phase. Insofar as subsong might involve rehearsal of memorized song themes, it could be viewed as bridging the gap between the perceptual and sensorimotor phases, alleviating any undue burden on the bird's memory.

The question of early rehearsal of learned song is moot, however, because no one has conducted a sound spectrographic study of the early stages in the development of singing. We undertook such an investigation in the swamp sparrow, *Melospiza georgiana*.

Male swamp sparrows brought into the laboratory as nestlings learn readily from taped songs of their species when these are played from the third to the eighth week of life. Full song develops some 9 months later and often contains a certain proportion of "syllables" that match components on the training tapes (*5*). The diverse morphology of natural

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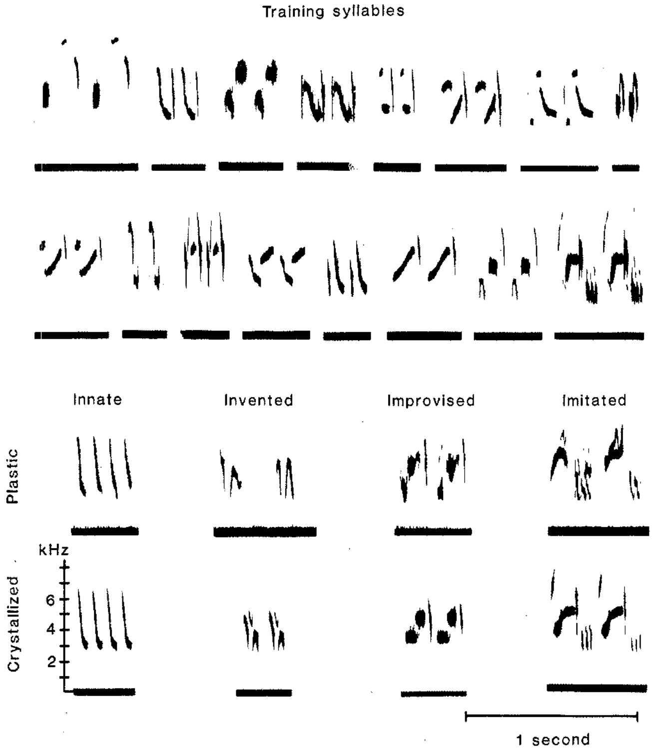

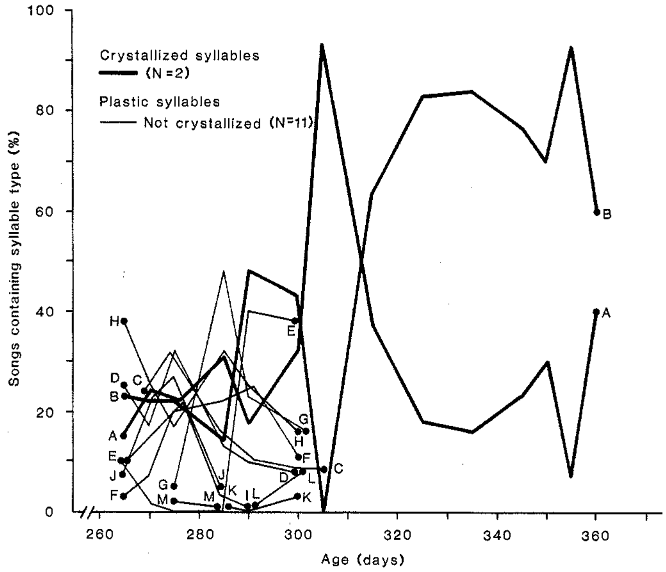

Fig. 1 (left). Pairs of the song syllables used for training the subjects. Also shown are pairs of syllables developed later (plastic and crystallized versions). These were classified as inventions, improvisations, and imitations. For comparison, a pair of innate syllables developed by an untrained swamp sparrow appears on the left. Fig. 2 (right). Changes in syllable usage with age in one male swamp sparrow. This bird crystallized two song types at 300 days, each with a single syllable type, *A* or *B*. Prior to this as many as 11 other syllable types were developed, only to be culled at the time of song crystallization. Syllables *A* and *B* are both copies of training syllables. Of the other syllables sung during plastic song, *C*, *D*, *E*, *F*, *H*, and *J* were copies; *G* and *I* were improvisations or poor copies; and *K*, *L*, and *M* were inventions.

swamp sparrow syllables permits choice of a great variety of training patterns. Exposure to different syllables in infancy results in different patterns of adult singing. The conclusion that songs are learned is based on this capacity to match acoustic models and on the abnormality of songs of birds reared without exposure to the species song (Fig. 1).

We reared 16 male swamp sparrows by hand in acoustic isolation from the species song. They were taken from the field as 2- to 10-day-old nestlings. The birds were trained for 40 days, beginning between 16 and 26 days of age. (Song stimulation before about 10 days of age has no detectable influence on song development. The songs of untrained males raised from the egg by foster parents have a similar syllabic structure to those of males taken as 10-day-old nestlings and reared without training.) The training songs consisted of a variety of experimentally modified arrangements of song syllables of this species and the closely related song sparrow (*Melospiza melodia*), arranged in bouts after the manner in which these birds typically sing (*5*). They were played twice a day, morning and evening. The training procedure faithfully followed methods used with success in previous years.

After training, the males were isolated in separate soundproof chambers. Beginning at about 95 days of age, their voices were recorded early in the morning once per week, continuing up to 1 year of age. Prior to this sporadic singing between 50 and 90 days was recorded and some was heard as early as 30 days. All this early singing was indistinguishable from that occurring around 100 days of age. Approximately 700 hours of recording yielded 235 hours of singing, with 15,056 songs.

All vocalizations other than call notes were edited out and analyzed by real-time spectrography (*6*). On the basis of visual inspection, singing was classified into seven categories. Stage 1, crystallized song, is the typical sterotyped male song. It consists of a 2-second string of identical repetitions of a multinote syllable at regular intervals (Fig. 1). As in nature, each male had a repertoire with an average of three song types. Stages 2 to 4, plastic song, are steps in the emergence of stereotyped syllables, separated by such criteria as stability of acoustic structure and regularity of the combinations in which they occur. Stages 5 and 6 are the variable and amorphous phases of "subplastic" song in which the rudiments of crystallized syllables can be recognized. They are transitional between plastic song and stage 7, subsong, which lacks defined syllables or other regularities.

After some singing from 100 to 150 days of age, the sparrows stopped from 160 to 238 days. Then, quite suddenly, one bird after another began to sing regularly. By 298 days all were singing. Sound spectrographic analysis revealed that the average age at which crystallized song emerged was 334 days (range, 300 to 350 days). Once crystallized, these songs remained stable for the rest of the season. In a subset of males studied during the second and third years of life, 31 crystallized songs remained unchanged, one was dropped, and one was slightly modified. There were no additions to any repertoire.

A survey of song development from the first subsong to crystallized song revealed a pattern to which all 16 birds conformed. On average, progression from subsong to subplastic song occurred at 285 days (range, 252 to 333 days). The average age at which plastic song began was 299 days. All males then advanced rapidly through the categories of plastic song—sometimes uttering several stages in a single day—to complete the process of song crystallization. Thus the first attempts of these males to reproduce memorized syllables began about 225 days after they last heard them, and rehearsal of particular syllables started about 2 weeks later.

Evidently sparrows commit song material heard in their first 2 months to memory and then keep it in storage, without rehearsal, for some 8 months.

Only in early adulthood, a time of rapid testicular growth and waxing androgen production, do they begin transforming portions of the memorized material into matching sound patterns.

Previously it was implicitly assumed that adult song is a reliable register of what a male bird has learned. The analysis of plastic song reveals that the birds developed much more than was needed for adult song. As already indicated, crystallized song repertoires in swamp sparrows typically consist of three syllables per male. The plastic song recorded only 1 week before crystallization incorporated an average of six different syllables per bird. Earlier in development there may be as many as 19 distinct syllables per male, with an average maximum of 12. Thus in plastic song a male swamp sparrow produces four times more syllables than are needed for the mature repertoire (Fig. 2). A total of 199 different syllables were identified in plastic song from the 16 males. Only 45 survived the crystallization process.

Comparison of the syllable types produced in plastic song with those heard in infancy was also revealing. Only 59 syllables—less than a third of those produced—were judged to be accurate copies of models. Of the remainder, 36 were construed as poor copies, perhaps modified by improvisation. This left 104 syllables unaccounted for. We conclude that these were inventions. Four of the 16 birds sang only invented and improvised syllables and 12 sang a mixture of imitated syllables. Invented and copied syllables mingle freely in plastic song, and a facility for syntactical rearrangement is evident in the many syllable recombinations that occur. Of the 45 syllables that were finally crystallized, 19 were copies of training songs, 19 were invented, and the rest were improvised or poorly copied. Thus, both inventions and imitations are winnowed as song develops.

Although imitation plays a crucial role in swamp sparrow song development, it evidently is not the only process involved. So far as we can determine, the invented syllables originated independently of the imitations and were not produced by progressive improvisation upon learned themes. They differed from the learned syllables in the smaller number of notes from which they were constructed (1.4 per syllable versus 2.8 for learned syllables). However, they were more complex than the innate song syllables of untrained swamp sparrows, which average 1.1 notes each (Fig. 1).

The process of singing from memory described here almost certainly occurs in wild swamp sparrows. A similar process probably occurs in the first year of life in many other songbirds. Temporal separation of the perceptual and sensorimotor phases of vocal ontogeny may be important in allowing cognitive mechanisms to operate on the memorized material. In sparrows these mechanisms appear to parse learned song material into syllabic multinote units that can then be recombined in novel syntactical arrangements by processes equivalent to phonological syntax in human speech (*7*). Finally, vocal invention makes a major contribution in birdsong ontogeny, even in a species such as the swamp sparrow, in which the impact of learning is pervasive. Many more syllables, both imitated and invented, are used in plastic song than in the final song patterns. This may be analogous to the overproduction of diverse speech sounds in the prespeech babbling of human infants (*8*).

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Electrotonic Coupling Between Pyramidal Cells: A Direct Demonstration in Rat Hippocampal Slices

Abstract. *Intracellular recordings from pairs of neurons in slices of rat hippocampus directly demonstrated electrotonic coupling between CA3 pyramidal cells. When two neurons were impaled simultaneously (as verified by subsequent double staining with horseradish peroxidase), current pulses injected into one cell caused voltage changes in other cells. These interactions were bidirectional. Fast prepotentials, historically thought to represent spike activity in dendrites, resulted from action potentials in other electrotonically coupled pyramidal cells. These data directly demonstrate electrotonic coupling between neurons in the mammalian brain and indicate that some fast prepotentials are coupling potentials. Coupling between pyramidal cells could mediate synchronization of normal rhythmic activity and of burst discharges during seizures.*

Several lines of evidence indicate that electrotonic coupling occurs between neurons in some areas of the mammalian central nervous system (*1*). The evidence has been indirect, however: (i) physiological results showing short-latency, collision-resistant depolarizations after antidromic activation of neurons coupled to the impaled cell (*2*) and (ii) observations of gap junctions (*3*), which are considered the ultrastructural substrate of electrotonic coupling. A direct demonstration of electrotonic coupling requires simultaneously impaling two neurons with two microelectrodes and injecting current into first one and then the other neuron to cause a voltage change in the uninjected neuron. Previously this has not been done in mammalian brain because of the difficulties of simultaneously impaling two coupled neurons. Electrotonic coupling in the hippocam-