

REPRODUCTIVELY DEPENDENT SONG CYCLICITY IN MATED MALE MOCKINGBIRDS (*MIMUS POLYGLOTTOS*)

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ABSTRACT.—Mockingbird (*Mimus polyglottos*) song has been demonstrated to function in the species' perennial territoriality. Data reported here suggest that this species' diverse song may also function intersexually in reproduction. Observations on the amount of song produced by identified males throughout the breeding season revealed a pronounced cyclicity in the occurrence of song. Further, song cyclicity was systematically associated with the nature of the breeding activity in progress. In each of six mated males, the amount of song increased substantially while the male was nest building. The amount of song decreased significantly during incubation and during the care of offspring. This relationship held even when the cycle of breeding activities was disrupted through nest loss; males resumed singing immediately, although losses often occurred during periods of very little song. Analyses indicated that the nest-building song burst did not result from the activities involved in nest construction itself but often preceded the first observed instance of nest building. Increased song during nest building cannot be explained by excess amounts of unoccupied singing time available to males not engaged in the care of offspring. The overall pattern of results indicates that Mockingbird song may function in reproductive as well as in territorial contexts. Further, the cyclic relationship between song and breeding activities suggests that song may constitute a mechanism by which the reproductive state of the female is rapidly reset in preparation for subsequent broods. *Received 11 February 1982, accepted 1 November 1982.*

SEVERAL lines of evidence suggest that the song of the Mockingbird (*Mimus polyglottos*) functions in the species' perennial territoriality. Michener and Michener (1935), for example, observed that peak territorial activity is correlated with the seasonal onset of song. More recently, Howard (1974) calculated a high positive correlation between territory rank and the size of the song repertoire in identified male Mockingbirds. Although both of the above reports are correlational, they are consistent with work demonstrating that playback of conspecific song evokes significant amounts of agonistic response in territorial residents. Playback of heterospecific song has no comparable effect, and, in the spring, playback of conspecific song is associated with the delayed production of song in the resident bird (Logan and Fulk MS). It is apparent, therefore, that, particularly during the spring (Logan and Fulk MS), Mockingbird song functions in territorial pronouncement.

In many species, diverse song may also serve reproductive functions that can be distinguished from the song's territorial function.

Kroodsma (1976), for example, demonstrated that female Canaries (*Serinus canaria*) exposed to males with larger song repertoires engaged in significantly more nesting behavior than females exposed to males with smaller song repertoires. Female Song Sparrows (*Melospiza melodia*) preferentially exhibit solicitation displays in response to conspecific male song; a more pronounced response is produced following playback of more diverse Song Sparrow song (Searcy and Marler 1981). Depending on the species, reproductive functions of song may exist in addition to the role of song in territoriality. One function need not preclude the other. For example, songs function in territoriality in most duetting species (Helversen 1978, Wickler 1980). In some species, however, duets also appear to function in pair bonding (Wickler 1980, Wickler and Seibt 1980). Wickler (1980) has suggested that the bonding function may have evolved from the song's territorial function.

Several considerations suggest that Mockingbird song may function intersexually in reproduction as well as in territoriality. Song di-

versity has been linked to reproductive functions in several species. Mockingbird song is extremely diverse, and, although intrasexual selection may be involved (Howard 1974), song diversity in this species exceeds that which might be expected solely on the basis of territoriality. Further, although Mockingbirds are perennially territorial, peak territorial activity occurs early in the spring and the fall (Michener and Michener 1935). In the spring, the song season lasts through July in the mid-temperate region, extending well beyond the period of peak territoriality. The duration of the song season is, however, coextensive with the period of spring breeding activities. Finally, song cyclicity has been closely associated with the cycle of breeding activities in several species (Davis 1958, Slagsvold 1977). Slagsvold (1977) reports that song peaks in over 20 species of birds are closely associated with the onset of egg laying. Single-brooded species are less likely to exhibit two song peaks, and species that typically produce a second brood have very high second song peaks. Mockingbirds commonly attempt several broods per season, and early accounts of Mockingbird song (Laskey 1935) allude to the song's cyclic occurrence at various stages during the breeding season. If Mockingbird song serves reproductive functions beyond those inherent in territoriality, the intersexual function of song may be reflected in the differential occurrence of song during the repeated cycling of spring reproductive activities. The present work attempts to relate the occurrence of Mockingbird song to the character of the reproductive activities occurring throughout the breeding season. The differential association of song with specific reproductive contexts would constitute strong preliminary evidence that, in the spring, Mockingbird song serves reproductive as well as territorial functions.

METHODS

I observed six mated pairs of Mockingbirds during the spring and summer of 1979 and 1980. The study area consisted of the urban residential community in and around the University of North Carolina at Greensboro. The area is densely populated with Mockingbird breeding territories, where numerous ornamental shrubs and trees provide abundant low-elevation nest sites. Within the area, *M. polyglottos* is sympatric with a number of other passerine species, including American Robins (*Turdus migratorius*), Blue

Jays (*Cyanocitta cristata*), Brown Thrashers (*Toxostoma rufum*), Northern Cardinals (*Cardinalis cardinalis*), and Rufous-sided Towhees (*Pipilo erythrophthalmus*).

Resident Mockingbirds begin to sing at the end of February, often before the arrival of mates. As such, song may occur well before and in the absence of other breeding activities. Evidence of the production of the first brood, therefore, provides the most valid indicant of the reproductive status of a mated pair. In an effort to assess reproductive status, and thereby to synchronize reproductive activities with the systematic observation of song, I began preliminary observations during March. By late April 1979, four pairs were chosen for systematic observation. Beginning in April 1980, observations of two of these pairs were resumed, and observations of two additional pairs were begun. Five males and 1 female among the six pairs chosen had been color-banded for previous work, and 4 of the 6 males were known to have held their territories for a period of at least 2 yr.

One-zero focal animal sampling (Altmann 1974) was conducted using two observers per pair during 60-min observation periods extending from 1 May to 1 August 1979 and from 2 April to 24 June 1980. The breeding cycle was divided into nest-building, incubation, nestling, and fledgling phases, and repeated hourly observation periods were conducted during each of the four phases of the breeding cycle. The periods were scheduled to meet a criterion per brood per pair of 4 h of observation during nest building, 6 h during incubation, and 6 h each during the nestling and fledgling phases of reproduction. Abortive reproductive efforts due to predation, weather conditions, etc., and substantial brood overlap in some pairs made it difficult to apply this criterion equally across pairs. Therefore, although the attempt was made to approximate these values as nearly as possible, different numbers of hours of observation were obtained for each pair. Within a reproductive phase, repeated observation periods were distributed equally across three time intervals: 0800–1000, 1100–1300, and 1600–1800.

Each hourly observation period was divided into 120 0.5-min time bins. The single occurrence of each of several behaviors in each time bin was recorded for both members of the mated pair. Where possible, I noted the sex of the bird responding; ambiguous or indeterminate instances were recorded as such. The following is a list of the behaviors measured and their characteristics: *song*—the behavior of primary interest, during the spring produced only by males; *feeding of offspring*—performed by both males and females in response to both nestlings and fledglings, often continuing for a period of 4–5 weeks; *other vocalizations*—especially including the chat and hew calls, commonly used in both conspecific and heterospecific agonistic interactions; *heterospecific and conspecific aggressive encounters*—aggressive encoun-

TABLE 1. Summary of observations collected on six mated pairs.

Bird	Total hours observed	Brood success	Dates of observation
C	30	2/5	3 May–24 July 1979
	18	2/2 ^a	19 May–24 June 1980
B	18	— ^b	May 1979 ^b
	28	2/3	5 April–14 June 1980
RC	35	3/3	1 May–29 July 1979
S	30	1/3	9 May–21 July 1979
U	38	2/3	2 April–23 June 1980
E ^c	26	0/3	10 April–6 June 1980
Total	223	12/22 (0.545)	

^a First brood not included—success unknown.

^b Observations interrupted—brood success unknown.

^c Mated bigamously after 25 May 1980—brood success reported only for first mate; two broods fledged successfully by second mate.

ters with other species (other passerines, squirrels, etc) and those involving other Mockingbirds, either mates, neighbors, or intruders; *nest building*—twigs carried to a nest site by either male or female; *nesting display*—twigs held prominently from a high perch, performed only by male; and *incubation*—performed only by the female.

Observation was initiated well within known territorial boundaries and only after one member of the mated pair had been sighted. A session was aborted if neither bird was sighted within 30 min or if, after the beginning of time-in recording, a time-out period exceeded 20 min. Time-out periods, defined by loss of visual contact with the bird, rarely exceeded 5–8 min. Using the procedure described above, I observed three unmated males for an additional 13 h during June and July 1979 and May 1981.

RESULTS

Each mated pair attempted several broods per season. This permitted repeated observation across broods of a given pair during most phases of reproduction. The number of broods attempted and fledged successfully and the total number of hours of observation per pair are presented in Table 1.

Brood overlap.—Assessment of the reproductive cyclicity of song was complicated by differing amounts of brood overlap across pairs. Substantial brood overlap was evident in five of the six pairs. In Pair RC, for example, brood 1 nestlings were fledged by 1 May 1979, but incubation of brood 2 eggs did not begin until 24 May, following the dispersal of the first group. Construction of the nest for the third brood, however, was first observed on 15 June. Brood 2 fledglings remained in the area, being

fed until they dispersed on about 7 July. The incubation of brood 3, therefore, occurred while brood 2 fledglings were still being fed. Similarly, in pair C, nest building, mating, and the initiation of incubation for brood 2 all occurred while fledglings of the previous brood were being fed by both parents. Although the amount of overlap varied from pair to pair, brood overlap and the recycling of breeding activities following the destruction of a nest were observed repeatedly. In no pair, however, was brood overlap so extensive that two broods required feeding simultaneously. It appears, therefore, that the overlap of successive broods is common in the Mockingbird. Further, the recycling of breeding activities does not follow an absolute time sequence. Rather, breeding activities are quickly recycled following the interruption of the sequence by nest failure.

Song cyclicity.—Observations of the distribution of song across the breeding season support Laskey's (1935) suggestion of considerable cyclicity in the occurrence of song (Figs. 1 and 2). The repeated waxing and waning of song was apparent in each of the males in the study.

Examination of Figs. 1 and 2 indicates that the cycling of song is differentially associated with certain breeding activities. Song increases dramatically during or just before nest building, decreases during incubation, and occurs very infrequently after nestlings have hatched. During brood overlap, the increase in song with nest building did not always occur (compare Figs. 1 and 2). Therefore, just as the amount of overlap varied across pairs, so did the impact

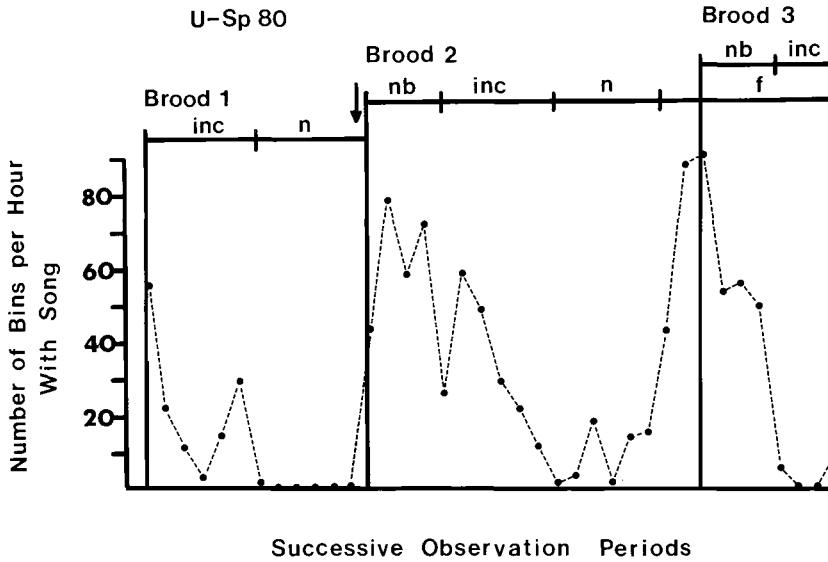


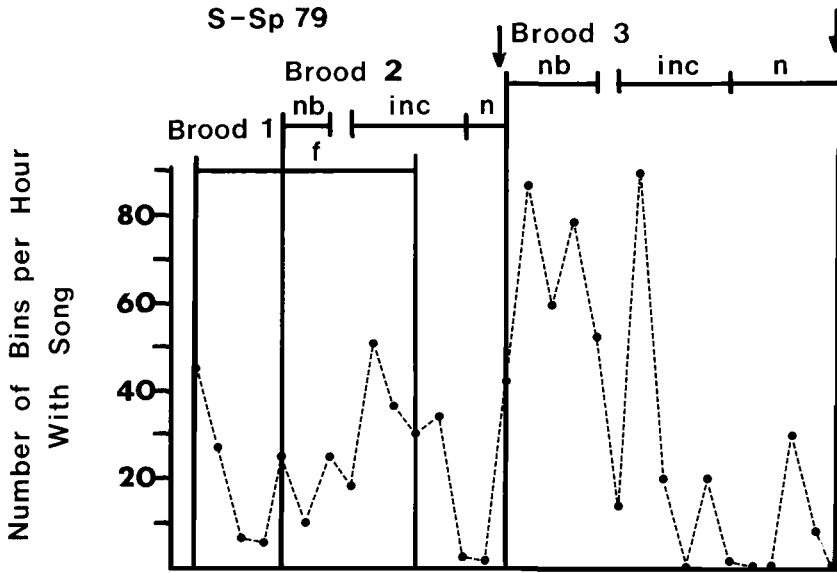
Fig. 1. Mean number of 30-s bins with song for one pair across successive observation periods ranging from 2 April to 23 June 1980. Horizontal lines above the points indicate the nature of the breeding activity in progress during the observation period. Parallel horizontal lines reflect brood overlap. The arrow indicates the occurrence of a nest loss. nb = nest building; inc = incubation; n = nestling phase; f = fledgling phase.

of overlap on the relationship between song and nest building.

Using the behaviors observed to define the breeding phase in progress, I calculated the amount of song occurring during the major phases of reproduction. Because of substantial amounts of brood overlap and frequent nest loss, few observations were obtained during the fledgling phase alone. Offspring are fed by the male and female for the duration of both the nestling and fledgling phases. Therefore, because these phases require comparable types of parental care, the two phases were combined for statistical analysis. Events occurring during the combined nestling and fledgling phases are referred to in the text as feeding ("Feed" in Table 2). Any behavior observed after the nest was begun but before the initiation of incubation was considered nest building, although the female probably lays her eggs during this period. The average amount of song occurring in each single condition as well as during the overlap of both incubation and feeding (I + F) and nest building and feeding (NB + F) is presented for each pair in Table 2. For all pairs, the song average was greatest during nest building, decreased during incubation, and was lowest during the feeding of

offspring. These values are paralleled during the overlap conditions, although during overlap the relationship is less consistent across pairs. A Friedman two-way analysis of variance by ranks (Daniel 1978) performed on the means of the four birds for which data are complete revealed no significant effect of subjects. To incorporate data for those birds for which some conditions were unrepresented, I therefore assumed independent samples and computed the Kruskal-Wallis one way analysis of variance by ranks (Daniel 1978) using the raw data for all subjects. There were highly significant differences in the amount of song occurring in different reproductive phases ($H = 114.2, P < 0.01$). Dunn's multiple comparisons test (Dunn 1964) indicated that significantly more song occurred during nest building as compared to feeding (NB/Feed), during nest building versus incubation, and during incubation versus feeding. These effects are paralleled in the overlap conditions. Only the nest building versus NB + F, incubation versus I + F, and incubation versus NB + F conditions failed to reach statistical significance.

It is possible that males sing more during nest building because, with no feeding required, more unoccupied time is available for



Successive Observation Periods

Fig. 2. Mean number of 30-s bins with song for a second pair across successive observation periods ranging from 9 May to 24 July 1979. Horizontal lines above the points indicate the nature of the breeding activity in progress during the observation period. Parallel horizontal lines reflect brood overlap. The arrows indicate the occurrence of nest losses. nb = nest building; inc = incubation; n = nestling phase; f = fledgling phase.

song. A comparison of the feeding alone and nest-building plus feeding (NB + F) conditions, however, suggests that this is not the case. Even while feeding and building, males sing significantly more than while feeding only ($P < 0.05$). Further, the nest building (NB) versus nest building plus feeding (NB + F) conditions did not differ significantly. In two males (U and B), more song occurred during nest building plus feeding than during nest building alone.

Informal observation suggests that mated Mockingbirds often trade off feeding responsibilities. During the incubation of one clutch, for example, the male provides virtually 100% of the food for the fledglings of the previous brood while the female incubates. Thus, it may also be possible that, although the male feeds at other times, during the overlap of nest building and feeding the male sings while the female takes on the major feeding responsibility. If this were the case, I could not necessarily conclude that song and feeding were temporally compatible during NB + F overlap. Fur-

ther examination of the data indicates, however, that this is not the case. I calculated the number of feedings by the male versus that by the female during those NB + F sessions in which the amount of male song was at or above the individual's mean for that condition. The average male/female feeding ratio equalled 1.48, indicating that, even with continuous song in progress, males fed almost 50% more often than did females during the NB + F overlap. Interestingly, when the amount of song during NB + F overlap dropped below the mean for that condition, the average male/female feeding ratio decreased to 0.81. These data suggest that singing and feeding are temporally quite compatible over the sampling period and that the observed differences are not due to the excess amounts of unoccupied singing time available to males with no offspring. Further, although song is dramatically decreased during feeding alone, this effect does not result from the inhibition of song produced by interaction with fledglings.

Nest loss.—The arrows situated at the tops of

TABLE 2. Average number of bins/h with song during various phases of reproduction.^a

Pair	Feed ^b	Inc	NB	I + F	NB + F
U	13.07 (14)	27.75 (12)	50.60 (4)	3.0 (4)	61.75 (4)
C ^c	12.51 (14)	37.40 (5)	60.0 (7)	36.0 (11)	47.83 (11)
B ^c	2.16 (12)	35.78 (9)	50.11 (9)	7.11 (9)	60.75 (4)
E ^d	11.67 (9)	27.90 (10)	62.86 (7)	—	—
R	10.42 (21)	29.75 (8)	—	14.0 (1)	20.25 (4)
S	9.27 (11)	32.67 (6)	67.50 (4)	36.0 (3)	26.0 (2)
\bar{x} =	10.23	31.88	57.67	16.06	43.68

^a Numbers in parentheses indicate the number of hours of observation on which the mean is based.

^b Column labelled "Feed" contains combined data from nestling and fledgling phases.

^c Data combined for 1979 and 1980.

^d Mated with two females during Inc and NB.

Figs. 1 and 2 indicate naturally occurring nest losses. Nest losses were quite common (see Table 1), usually occurring either during the incubation or nestling phases of the breeding cycle. As a consequence, song was relatively infrequent before nest loss. In each pair, however, nest loss was accompanied by a dramatic increase in song, with an almost immediate resumption of nest building. Analyses of the amount of song occurring in the single hourly observation period conducted before versus after destruction of the nest reveal a statistically significant increase in the amount of song produced following nest destruction [t (df, 8) = 4.24, $P < 0.01$; see Table 3]. Examination of Table 3 indicates that song increased following nest losses occurring either during the incubation or the nestling phase of breeding.

Nest song.—The occurrence of Mockingbird song is not readily associated with specific local contexts. Birds often sing from very high perches for extended periods of from 10 to 30 min without apparent reference to events going on around them. I have observed one situation, however, in which a male's song occurs within the immediate context of the bird's other activities. This again involves nest building, and I provisionally refer to the song noted as nest song. Nest song was observed in each of the six males in the study during the breeding seasons of both 1979 and 1980. In two males as many as 15 instances of nest song were noted,

TABLE 3. Number of bins per hour with song before and after nest destruction.

Pair ^a	Before	After
B (I)	0	68
U (N)	0	44
C (I)	37	61
C (I)	32	67
S (N)	1	43
\bar{x} =	14.0	56.6 ($t = 4.24, P < 0.01$)

^a Letters in parentheses indicate the breeding phase during which nest destruction occurred.

with up to 6 occurring in a single hourly observation period. In each case the male carried nesting material into a partially constructed nest, worked with the material at the nest for as long as 60 s, and then remained at the nest for an additional brief period during which he sang from the nest. Once song began, the bird remained at the nest for from 30 to 120 s, singing only a few phrases. Typically, the male ceased singing and left the nest within 30 s of the onset of nest song. Not all trips to the nest were accompanied by nest song, and during some periods in which nest building was in progress no nest song occurred at all. On at least two occasions one subject, which was singing, flew to the nest with no nesting material, continued singing on the nest, and left after as few as 30–60 s. Although nest song was occasionally preceded by extended song before the nest visit, this was by no means always the case (see Table 4). In 49% of the cases, nest song was not preceded by extended song in progress. Nest song may, therefore, represent something more than simply the intrusion of extended song into nest building activities.

TABLE 4. The occurrence of nest song in Mockingbirds.

Bird	NB ^a	NS ^b	NS ^c
S	11	7	3 (3)
C	16	1	1 (1)
B	30	18	11 (5)
E	7	1	1 (1)
RC	2	2	1 (1)
U	27	15	5 (5)

^a Total number of trips to the nest during hourly periods in which nest song was observed.

^b Observed instances of nest song.

^c Number of instances of nest song not preceded by extended song of at least 3 min in duration. Numbers in parentheses indicate the total hours of observation on which these figures are based. Periods with nest building but no nest song are not included.

TABLE 5. Comparisons of the average amount of song produced by mated versus unmated males in comparable periods during the breeding season.^a

	1-7 June 1979		5-15 July 1979		17-24 April 1980 (81 ^b)	
	M	U	M	U	M	U
	32.5 (2)	39.0 (4)	11.0 (2)	49.5 (4)	0.0 (1)	64.8 (5)
	60.8 (4) ^c		41.4 (5) ^c		77.0 (1) ^c	
	65.6 (5) ^c		2.7 (3)		7.3 (3)	
	1.6 (5)		—		—	
Overall means	41.2		18.4		28.1	

^a Values in parentheses indicate the total hours of observation on which the means are based. M refers to mated males; U refers to unmated males.

^b Data on unmated males were collected during the 1981 breeding season.

^c Indicates samples during which nest building was in progress.

Females often aid the male in building the nest, although they rarely engage in as much building as the male. Although more observation will be needed to verify these points, the occurrence of nest song does not seem to be related to the degree of the female's involvement in nest building. Males were just as likely to engage in nest song whether or not the female had participated in building. Further, males apparently produced nest song whether or not the female was visible at the time the male entered the nest.

Unmated males.—A total of 13 h of observation was conducted on three unmated males during the months of April (1981) and June and July (1979). Because observations were not conducted throughout the season, no calculations of song cyclicity were possible for these birds. However, the average number of bins with song per hour for each bird (see Table 5) indicates that, although song production varied considerably, the amount of song produced by unmated males may be comparable to that produced by mated males during nest building. Further, unmated males appear to engage occasionally in longer periods of uninterrupted song than is seen typically in mated males. Song periods approaching one full hour in duration with no pauses exceeding 60 s were not uncommon in the unmated males. In over 150 h of observation, however, extended song periods in mated males rarely exceeded 15 min in duration.

To evaluate the effect of time during the season on the amount of song produced, I calculated the average amount of song produced by mated males during those weeks in which song samples were taken from each of the unmated males. Although based on few data, the results

suggest that mated males do not necessarily produce extended song during those periods in which considerable song is produced by unmated males (Table 5). During 5-15 July 1979, for example, the average amount of song produced by three mated males was 18.35 bins with song. For the same week, one unmated male produced an average of 49.5 bins with song. It should be noted that during this period the mated males represent several phases of reproductive activity. One, for example, was nest building; the others were not. In the building male, the amount of song produced was comparable to that seen in the unmated male; the others exhibit much less song. These results indicate that the cyclicity of song is not the result of a biological clock. They also indicate that, although extensive song may be related to nest building in mated males, comparable amounts of song can occur in the absence of mating activity.

DISCUSSION

Strong evidence of the communicative value of a signal requires a demonstration that the signal either directly or indirectly alters the behavior of a receiver. The influence of male song on reproductive behavior has been documented in this fashion in a number of passerine species. In the Song Sparrow, for example, playback of more diverse male song elicits more copulatory solicitation by females than does playback of either heterospecific song or less diverse Song Sparrow song (Searcy and Marler 1981). Weaker evidence regarding the communicative value of a signal may be obtained from the context in which that signal occurs (Payne 1979). In effect, context provides a neces-

sary but not sufficient condition for determining the content of a signal. The results reported above indicate that during the breeding season mated male Mockingbirds are more likely to sing while nest building than during any other phase of reproduction. In addition, when breeding activities are interrupted through nest loss and the nest-building context is abruptly reintroduced, the amount of male song increases substantially. Although data from unmated males indicate that nest building does not provide the only context in which extended song occurs, both findings reveal that Mockingbird song and nest building are highly correlated. These results therefore constitute support for the conclusion that Mockingbird song functions in reproductive as well as territorial signalling.

If song produced during nest building functions in reproductive signalling, then it may do so either by its effect on other males or other females. Insofar as is known, there is very little competitive or cooperative interaction among breeding male Mockingbirds once territories are established. Both mates and territorial residence are established for life, and interactions among mated males are usually restricted to territorial pronouncement and defense (Michener and Michener 1935). It is possible that the increased song occurring during nest building functions in territorial defense of the nest site itself. Although this alternative cannot be ruled out at this time, observations of the locations of nests render it unlikely. If defense of the nest site were of prime importance in the nest-building song burst, one would predict either that most nest sites would be as close to the center of the territory as resources permit or that favored song perches would be near the nest site. My observations indicate that neither was the case for the pairs described. In 5 of the 6 pairs at least one nest site was situated very close to the territorial boundary. On one occasion, two adjacent pairs positioned nests on either side of their common boundary, within 2 m of each other. Both the natural history of this species and our knowledge of the reproductive function of male song in other species, however, suggest that extended male song might affect the female. Conclusive evidence of the impact of male song on female behavior is available for the Brown-headed Cowbird (*Molothrus ater*) (King and West 1977, West et al. 1979), the domestic Canary (Hinde

and Steele 1976, Kroodsma 1976), the Zebra Finch (*Poephila guttata*) (Miller 1979), the Song Sparrow (Searcy and Marler 1981), and the Budgerigar (*Melopsittacus undulatus*) (Brockway 1965, Hinde and Steele 1978). In each of these species reproductive functions are strongly implicated. Mockingbirds are a perennially monogamous, multibrooded species in which the male makes considerable investment in the care of offspring. These conditions might make individual recognition by song (e.g. Zebra Finches), increased fertility, the facilitation of breeding activities (e.g. Canaries, Song Sparrows), or the strengthening of the pair bond through song highly adaptive. At present it is impossible to determine which, if any, of these functions may be served by Mockingbird song.

The data reported here do not provide a definitive indication of what factors might stimulate the increase in song during nest building. Several possibilities may be ruled out, however. The amount of song occurring during the overlap of NB + F indicates that extended song may occur in the presence of fledglings. The dispersal of offspring from the previous brood is not, therefore, a necessary condition for the increase in song. Male/female feeding ratios calculated during NB + F indicate that interaction with fledglings, rather than inhibiting song, may be associated with increased song. These findings indicate that neither the disappearance of offspring nor the absence of interaction between the male and his offspring is systematically related to the nest-building increase in male song. The abrupt increase in song following nest loss, however, strongly suggests that one or more stimuli associated with the cycle of breeding activities initiates the nest-building song burst.

The activities involved in building the nest might themselves provide the stimulus to sing. Further examination of the data, however, indicates that the increase in song frequently precedes the first observed occurrence of nest building. Because observations were initiated at the first occurrence of nest building, I have no data on the amount of song that preceded nest building in the absence of brood overlap. In 5 of the 8 instances in which nest building occurred during NB + F overlap, however, the amount of song increased steadily in the three hourly observation periods immediately preceding the first observed occurrence of nest building. For example, in bird U song in-

creased from 15 through 43 to 87 bins per hour with song before any observed instance of nest building. In the next observation period, when nest building was first observed, the male sang during 90 of the 120 time bins. Similar increases in song before the first observed occurrence of nest building were evident in four other males in the study. The extended song evident during nest building, therefore, does not result from the nest-building activity itself. Further, the abrupt increase in singing following nest loss indicates that the passage of time is not a necessary factor in initiating song. While time may play a role, some additional factor must be responsible for the rapid increase in song following nest loss.

Hypotheses regarding the functions of large song repertoires are of on-going interest in the study of bird song (e.g. Krebs and Kroodsma 1980). The problem is particularly pertinent in the Mimidae, where the typical male repertoire is extremely large (Boughey and Thompson 1981, Kroodsma and Parker 1977, pers. obs.) and may increase with age and experience. Howard (1974) has suggested that the large repertoires of Mockingbirds are the result of intrasexual selection for high-quality territories, which, in turn, quickly attract mates. Such intense intrasexual selection would seem unlikely, however, in a perennially monogamous species in which the male establishes a life-long territorial space in his first or second year and invests considerable time and energy in the care of offspring (Trivers 1972). In two species, large repertoires have been shown to be more effective than small repertoires in the stimulation of female reproductive behavior and/or fertility. Kroodsma (1976) has demonstrated that female Canaries exposed to the songs of males with larger repertoires engage in significantly more nesting behavior and lay more eggs than females exposed to smaller song repertoires. Marler and Searcy (1981) have reported a similar effect of repertoire size on the frequency of copulatory solicitation in female Song Sparrows. The work of Hinde and Steele and their colleagues suggests several mechanisms by which male song might produce its effects. They have demonstrated that in both Canaries and Budgerigars [see Hinde and Steele (1978) for review] male song may alter female reproductive behavior by influencing the production and the effectiveness of gonadal steroids. In Mockingbirds, nest building is pri-

marily, though not exclusively, the responsibility of the male. Mating usually occurs following nest building, and the song burst associated with nest building may, therefore, permit the extensive Mockingbird repertoire to alter either the receptivity or the fertility of the female following nest building. Either might result in more broods per season or in larger broods, and the changes produced by more diverse song would, therefore, promote very rapid selection for large song repertoires.

Laskey's (1935) suggestion of considerable cyclicity in the occurrence of Mockingbird song during the spring is confirmed by the observations reported here. Reproductive cyclicity in song has been reported in several avian species (Davis 1958, Slagsvold 1977). Slagsvold's work (1977) indicates both that song peaks often precede egg laying and that cyclical singing (indicated by second song peaks) is far more typical of multibrooded species. In any multibrooded species subject to considerable predation or nest loss, a mechanism for resetting the complicated endocrine interactions essential for the normal cycle of events would be adaptive. In Mockingbirds, song and nest building recur together in cyclic fashion throughout the breeding season, and singing does not appear to result from activities associated with nest construction itself. Evidence from other avian species indicates that male vocalizations may have considerable impact on the female's endocrine system. Taken together, these findings raise the possibility that in Mockingbirds song may constitute one means by which the female's reproductive system is reset in preparation for a second and subsequent broods. This possibility, however, would place certain requirements on the communicative interaction between male and female. For example, other males frequently sing within earshot of a given female. To prevent neighboring males from disrupting the reproductive synchrony of the mated pair, females must be able to discriminate specific features of their mates' songs. Although the intensity of song may provide the basis for discrimination (Richards 1981), idiosyncratic structural features of song might provide the more reliable cue, because both song and nest construction may occur near territorial boundaries. Each of the above considerations requires demonstration that male song alters either the reproductive state or the behavior of the female. Al-

though the data presented do not provide such a demonstration, they do constitute evidence that Mockingbird song serves reproductive functions beyond those inherent in territorial signalling. The specific nature of such functions remains to be determined.

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