

YEARLY AND SITUATIONAL CHANGES IN THE  
ESTIMATE OF REPERTOIRE SIZE IN  
NORTHERN MOCKINGBIRDS  
(*MIMUS POLYGLOTTOS*)

KIM C. DERRICKSON<sup>1</sup>

*Leidy Laboratory, Department of Biology, University of Pennsylvania,  
Philadelphia, Pennsylvania 19104 USA*

**ABSTRACT.**—The singing behavior of 4 male Northern Mockingbirds (*Mimus polyglottos*) was studied during 1980 and 1981. Over 10,000 song bouts (repetition of a particular song type) were analyzed spectrographically. Between 102 and 412 distinct song types were identified for each male in a given year. Many of these song types (25.8–57.4%) occurred only once in this sample of singing behavior. Repertoire size was estimated by fitting an exponential curve to a cumulative plot of distinct song types as a function of consecutive bouts sampled. The resulting asymptote was the estimate of repertoire size. Sequences of at least 50 consecutive bouts were used in estimating repertoire size. The technique of using consecutive bouts was required because of the high proportion of rare song types. Several estimates were made for each male and resulted in mean repertoire size estimates of 100–200 song types for the four males. Long sequences (125–150 bouts) of consecutive bouts are preferred to estimate repertoire size accurately. In addition, the social situation in which the singing behavior occurred can alter significantly the estimate of repertoire size. For example, estimates produced from singing during patrolling or countersinging were smaller than estimates generated from singing while associating with a female.

The repertoire size estimate increased between 1980 and 1981 for 3 of 4 males. The one male not showing an increase spent much time patrolling and interacting with neighboring males before dying early in 1981. These results are consistent with the impression that repertoire size increases with age. Received 3 April 1986, accepted 4 October 1986.

THE number of songs typical of an individual's repertoire differs greatly among bird species. Males of some avian species sing a single song throughout the breeding season. For example, Ovenbirds (*Seiurus aurocapillus*; Weeden and Falls 1959), Indigo Buntings (*Passerina cyanea*; Emlen 1971), Field Sparrows (*Spizella pusilla*; Goldman 1973), White-throated Sparrows (*Zonotrichia albicollis*; Borror and Gunn 1965, Falls 1969, Lemon and Harris 1974), and Common Yellowthroats (*Geothlypis trichas*; Wunderle 1978) sing a single song.

Other passerines have larger repertoires. Hartshorne (1973) and Dobson and Lemon (1975) estimated that individuals of three quarters of all songbird species have more than a single song type. Individual males of many species utter between 2 and 10 distinct song types. For example, Common Chaffinches (*Fringilla coelebs*; Pickstock and Krebs 1980, Slater

1981), Great Tits (*Parus major*; Krebs 1971), and Striped-backed Wrens (*Campylorhynchus nuchalis*; Wiley and Wiley 1977) have approximately 5 song types in their repertoires, while Western Meadowlarks (*Sturnella neglecta*; Falls and Krebs 1975, Falls and d'Agincourt 1981) and Song Sparrows (*Melospiza melodia*; Harris and Lemon 1976, Searcy et al. 1981) typically average 10 song types. Bradley (1980) reported a mean repertoire size of 5.2 song types for White-eyed Vireos (*Vireo griseus*). However, he suspected that most males actually sing about 10 song types, and his low estimate reflected insufficient sampling—always a potential problem.

Larger repertoires are documented for Bewick's Wrens (*Thryomanes bewickii*: 13–20 song types; Kroodsma 1974), Red-eyed Vireos (*Vireo olivaceus*: mean = 39.4 song types; Borror 1981), eastern populations of Marsh Wrens (*Cistothorus palustris*: over 50 song types; Canady et al. 1984), and Eastern Meadowlarks (*Sturnella magna*: over 54 song types; Falls and d'Agincourt 1981). Borror (1981) also noted the sampling

<sup>1</sup> Present address: Department of Zoological Research, National Zoological Park, Smithsonian Institution, Washington, D.C. 20008 USA.

problem: "samples of a few hundred, or even thousand, songs may not yield a Red-eyed Vireo's complete repertoire, or tell fully how that repertoire is used." This problem becomes more exaggerated in species in which males have large repertoires. Individual males with over 100 distinct song types have been documented in the Sedge Wren (*Cistothorus platensis*; Kroodsma and Verner 1978), western populations of the Marsh Wren (Verner 1975, Canady et al. 1984), Rock Wren (*Salpinctes obsoletus*; Kroodsma 1975), European Robin (*Erithacus rubecula*; Bremond 1968), and European Nightingale (*Luscinia megarhynchos*; Hultsch and Todt 1982). Kroodsma and Parker (1977) estimated that male Brown Thrashers (*Toxostoma rufum*) sing up to several thousand different song types.

Individual Northern Mockingbirds (*Mimus polyglottos*) also have extraordinarily large repertoires. Estimates of size vary. Howard (1974) reported mean repertoire sizes of individuals in two populations in Texas as 77.0 and 93.9 "syllable patterns" (= song types) per male. Estimated repertoires of individuals ranged from 45 to 150. Selander and Hunter (*in* Wildenthal 1965) estimated the repertoire size of two birds in Texas as 66 and 96 syllable patterns. Wildenthal (1965) estimated that two Kansas mockingbirds had repertoires of 244 and 213 syllable patterns, and one Florida mockingbird approximately 190.

Many hypotheses have been advanced to explain the existence of several song types in a repertoire, including individual recognition (see Falls 1982 for review), sexual selection (Kroodsma 1976; Catchpole 1980; Yasukawa et al. 1980; McGregor et al. 1981; Searcy and Marler 1981, 1984; Kroodsma and Canady 1985), territorial defense (Howard 1974; Krebs 1977a, 1978; Slater 1981; Kroodsma and Canady 1985), antihabituation (Hartshorne 1956, 1973; Krebs 1976; Kroodsma 1982), Beau-Geste (Krebs 1977b, Yasukawa 1981), differential provisioning of information (Smith 1970; Smith et al. 1978; Derrickson 1985, 1987), and a perceptual mechanism, the ranging hypothesis (Morton 1982, 1986).

Before attempting to associate the variation in repertoire size among individuals with other aspects of their reproductive biology, it is essential to estimate accurately each individual's repertoire. This can be especially difficult for species with large repertoires. One method

(Wildenthal 1965) plots the number of new repertoire components in a sample of song against the total number of components sampled. The asymptote of an exponential curve fitted to this plot is the estimate of repertoire size. Kroodsma (1982) discussed two conditions for this exponential curve to model accurately the singing behavior of an individual. First, the number of song types in the repertoire must remain constant during the sampling period. When sampling periods are relatively short this is not likely to be a problem, except when using a random sampling scheme such as used by Howard (1974), which will underestimate rare song types. Second, the song types must be presented randomly by the bird. This is often not the case. The next song type may depend on the preceding song type or song types (Lemon and Chatfield 1971, Falls and Krebs 1975, Dobson and Lemon 1979). In addition, songbirds may present a larger fraction of their repertoire during a shorter interval than would be expected (Verner 1975, Dobson and Lemon 1977) by actively avoiding reuse of a song type until many other song types have been presented. Further, some song types are relatively common while others are rare (Derrickson 1985, MS). Howard's (1974) random sampling technique for mockingbird song results in a separation of sampled songs by many intervening songs. This makes it difficult to document first-order Markov processes (Derrickson unpubl. data). As noted above, random sampling also misses many rare song types, causing underestimation of the size of the repertoire (Kroodsma 1982).

I show here that for a species with a large repertoire, the Northern Mockingbird, repertoire size estimates differ depending on the social situations sampled. I also show how the estimates of repertoire size differ between years for four males.

#### METHODS

Research was conducted at Tyler Arboretum, Lima, Pennsylvania, between fall 1979 and spring 1983. Each year 6-10 mockingbird pairs were studied. Half of these individuals were captured and banded with a unique color combination of plastic leg streamers. The focal-individual sampling technique (Altmann 1974, Dunbar 1976) was used. Individuals were observed in a random order except when behavioral and situational circumstances required that one in-

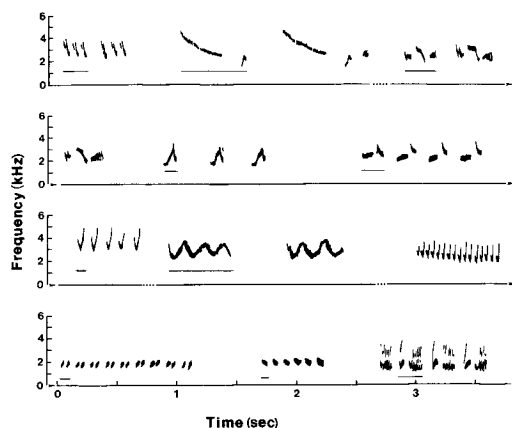


Fig. 1. Spectrograms of early spring song by a male Northern Mockingbird. Fifty-six songs are organized into 11 bouts of different song types. The first complete example of a song type is underlined.

individual be monitored more closely. Observations were made mainly from one-half hour before sunrise until noon. Occasionally, observations were made during the afternoon, evening, and night. Vocalizations were recorded with a Marantz Superscope CD-330 professional dual track cassette tape recorder and a Gibson P-200 parabolic microphone. A Superscope model E-5 cardioid microphone was used to record a continuous description of the bird's behavior, location, orientation, and other contextual information. More detailed descriptions of the study site and field techniques are provided elsewhere (Derrickson 1985, MS).

The singing behavior of four male mockingbirds was analyzed in detail during 1980 and 1981. Songs occurring during different social situations were analyzed using a Kay Elemetrics 6061B Sona-Graph or a Princeton Applied Research real-time sound spectrum analyzer. Figure 1 depicts 56 songs traced from spectrograms (time intervals within and among songs accurately portrayed) as an example of singing by a male mockingbird during early spring. They are organized into 11 bouts of different "types." I define a song type as a single vocalization or a group of vocalizations (1) in which the time intervals between the units of the group are shorter than the time intervals between groups, and (2) that is uttered in a *consistent* (although not completely identical) form on every occurrence by a particular individual. Typically, mockingbirds repeat a song of one type several times (i.e. in a bout) before switching to another type. Bout length is defined as the number of repetitions of a song before switching. In Fig. 1, the bout lengths are 2, 2, 3, 3, 4, 5, 2, 16, 9, 6, and 4 (=56 songs) for the 11 song types. In a few bouts, such as the last one in Fig. 1, only a portion of the song type may be given

at the beginning or end of the bout. That a particular song type might be repeated two times in one bout and three times in a subsequent bout made identifying what constituted the song type very easy. A more complete description of the classification scheme was given by Derrickson (1985, MS). Individual song types were identified and classified in a numeric directory for each male. I described sequences of song type bouts with this classification system.

Two methods were used to describe repertoire size. One method involved sampling intensively (see Table 1) the singing behavior and produced a single estimate for each bird in both years. The second method involved generating a plot of new song types as a function of bouts sampled during a singing session and fitting a curve to this plot. The asymptote of the curve was used to estimate repertoire size. One major advantage of this technique is that shorter sequences of songs were required, and hence several estimates were generated for each bird in both years. However, this method has several disadvantages and should be used cautiously. Estimates derived from this second technique were used in all the analyses reported here unless otherwise noted.

Repertoire size was estimated from sequences consisting of over 50 consecutive bouts. Approximately one third of the 65 sequences used in this analysis were of fewer than 100 consecutive bouts. Initially, the number of distinct song types increased linearly as singing proceeded. Subsequently, the rate at which new song types were introduced decreased asymptotically. The repertoire curve obtained by plotting the number of distinct song types as a function of the number of bouts sampled was accurately approximated by an exponential curve of the form (Wildenthal 1965):

$$n = N \cdot (1 - e^{-T/N}),$$

where  $n$  is the number of distinct song types in the sample,  $T$  is the total number of bouts sampled, and  $N$  is the number of different song types in the total repertoire. The asymptote,  $N$ , was estimated for each sequence using the least-squares nonlinear regression procedure. The Marquardt iterative method option was specified (SAS 1982).

For each estimate, the bird producing the song, the year, and the social situation were recorded. Eight social situations were used: before a female arrived on his territory, associating with the female in the center of the territory, being near the border while his mate was nearby, nest building, being near the nest and the female, nestling and fledgling breeding stages, patrolling and countersinging, and singing at night. ANOVAs tested if repertoire size estimates differed among males, between years, or among situations. Tukey's studentized range test was used to compare mean estimates among birds, between years, and among situations.

TABLE 1. Mockingbird song repertoires. The number of distinct song types, number of bouts inspected, and percentage of song types that occurred only once are given for 4 males during 1980 and 1981.

| Individual and year |      | No. of distinct song types | No. of bouts inspected | Percentage of song types occurring only once |
|---------------------|------|----------------------------|------------------------|--|
| A                   | 1980 | 412                        | 2,698                  | 30.60  |
|                     | 1981 | 319                        | 3,358                  | 26.60  |
| B                   | 1980 | 346                        | 1,632                  | 27.86  |
|                     | 1981 | 263                        | 861                    | 39.00  |
| C                   | 1980 | 196                        | 721                    | 25.76  |
|                     | 1981 | 145                        | 465                    | 37.90  |
| D                   | 1980 | 102                        | 168                    | 57.43  |
|                     | 1981 | 244                        | 815                    | 33.06  |

### RESULTS

The number of distinct song types produced by 4 males during the 1980 and 1981 breeding seasons is presented in Table 1. Repertoire size estimates using this approach ranged from 102 to 412 song types per male. The estimated repertoire size declined between 1980 and 1981 for 3 males and increased for the remaining male. Furthermore, the ranking of birds on the basis of this measure of repertoire size showed no relationship to minimum known age, breeding success, or pairing date for both years. The sampling effort, as measured by the number of bouts sampled, also is listed. There was a significant correlation ( $r = 0.826$ ,  $df = 6$ ,  $P < 0.05$ ) between the number of distinct song types and the sampling effort. However, a plot of these data showed the number of distinct song types began to level off after approximately 1,500–2,000 bouts had been sampled. Also listed in Table 1 is the percentage of song types that occurred only once. As expected, as the sampling effort increased, the proportion of song types that occurred only once decreased. Even for intensely sampled individuals, however, the proportion never fell below 25%. Thus, over one quarter of all song types sung by male mockingbirds are extremely rare.

The exponential model used to estimate repertoire size fit the data extremely well and explained consistently over 99% of the total variance in each of the 65 bout sequences analyzed. This was not unexpected because the data points were not independent from one another. The

TABLE 2. Mean and standard error of the estimated repertoire size for 4 males during 1980 and 1981. The number of estimates used is given in parentheses.

| Individual | Estimated repertoire size |            |        |            |  |  |
|------------|---------------------------|------------|--------|------------|--|--|
|            | 1980                      |            | 1981   |            |  |  |
|            | Mean                      | SE         | Mean   | SE         |  |  |
| A          | 143.94                    | 25.82 (14) | 194.69 | 17.38 (19) |  |  |
| B          | 159.42                    | 23.11 (10) | 190.19 | 43.69 (9)  |  |  |
| C          | 202.71                    | 25.24 (5)  | 111.21 | 11.32 (3)  |  |  |
| D          | 84.46                     | 31.59 (2)  | 171.76 | 38.41 (3)  |  |  |

mean and standard error of the repertoire size for the four males during 1980 and 1981 estimated using this technique are presented in Table 2. Results from a two-way ANOVA for differences in repertoire size estimates among males and between years showed no significant difference among males ( $F = 0.27$ ,  $df = 3$ ,  $P > 0.10$ ) or between years ( $F = 1.97$ ,  $df = 1$ ,  $P > 0.10$ ). The interaction term was not significant. The mean estimated repertoire size increased between 1980 and 1981 for 3 of the 4 males. These increases between years were not significant when analyses were performed on each male. The estimated repertoire size of male C decreased significantly in 1981 ( $F = 6.97$ ,  $df = 1$ ,  $P < 0.05$ ). The 1981 estimate might be inaccurate because he died 3 weeks into the breeding season, just when the female had initiated incubation. Also during this period he spent more time patrolling his borders and interacting with neighboring males than he had in previous years. These results, although not significant, are consistent with Howard's (1974) speculation that repertoire size increases with age. Furthermore, the ranking of birds on the basis of this estimate of repertoire size was identical to the ranking based on minimum known age, pairing date, and number of young fledged in 1980. This correlation did not exist in 1981.

The ranking of males by repertoire size using the estimation procedure was identical to the ranking produced by intensive sampling in 1981. In 1980 the male with the largest repertoire size as judged by intensive sampling was ranked third with the estimation procedure, and the male ranked third through intensive sampling was ranked first with the estimation procedure.

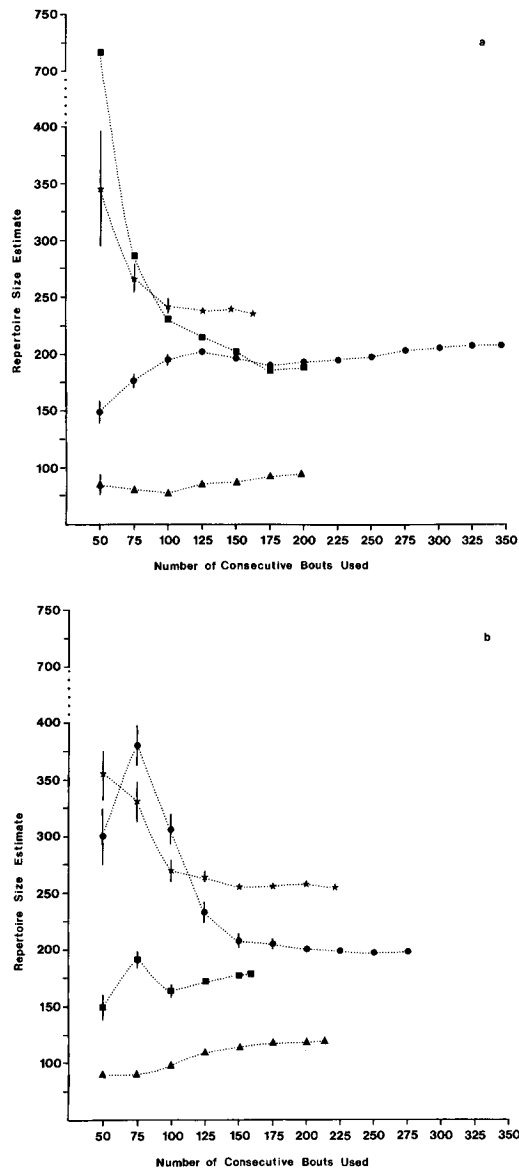


Fig. 2. Reliability of repertoire size estimates. Changes in the repertoire size estimate ( $\pm 95\%$  confidence limits) for 8 (4 displayed in part a and 4 in part b) singing sessions as more consecutive bouts are used to estimate the repertoire size. Each type of symbol represents one sample.

One potential problem in estimating repertoire size by the exponential model involves sample size. Repertoire size estimates based on fewer than 75 successive bouts ranged from 18 to 345 song types. Estimates calculated on samples of 150 or more consecutive bouts ranged

TABLE 3. Mean and standard error of the estimated repertoire size occurring during different social situations. Situations followed by (F) involved the male associating with his mate. The number of estimates used is given in parentheses.

| Situation                               | Estimated repertoire size |       |      |
|---|---------------------------|-------|------|
|   | Mean                      | SE    |      |
| Associating with female (F)             | 208.68                    | 21.05 | (19) |
| Near female and nest (F)                | 201.01                    | 25.28 | (13) |
| Nest building in presence of female (F) | 169.22                    |       | (1)  |
| Before female arrives                   | 168.82                    | 31.73 | (9)  |
| Patrolling, countersinging              | 137.05                    | 15.49 | (15) |
| Near border with female (F)             | 104.48                    | 20.35 | (3)  |
| With nestlings or fledglings            | 83.10                     | 17.74 | (5)  |
| Night singing                           | 82.10                     | 7.22  | (3)  |

from 94 to 256 song types. The variance in the repertoire size estimate thus decreased as longer samples were used.

The reliability of the repertoire size estimate decreased as fewer consecutive bouts were used to calculate the estimate (Fig. 2a, b). The eight samples that had the largest number of consecutive bouts are depicted. For each sample, as the number of consecutive bouts used to calculate the repertoire size estimate (obtained by consecutively deleting the last 25, 50, 75, etc. song types from the sample) was decreased, the estimate began to differ from the estimate calculated by using the total sample. With fewer bouts used, 4 of the 8 samples predicted radically larger repertoire sizes, 2 gradually predicted smaller, and the remaining 2 varied unpredictably as the sample size declined. Accurate estimates appear to be achievable if at least 125–150 consecutive bouts are used, because all the curves become nearly flat in this region.

Another potential problem in estimating repertoire size involves the concurrent social situation. An individual male generates different repertoire size estimates depending on the social situation. The top three curves in Fig. 3 represent singing sessions that occurred while the males were associated closely with their respective females in the center of their territories. The bottom three curves (for two of the above males), described in descending order, represent a male singing along a border, a male engaged in a countersinging session with a neighboring territorial male, and an unmated

male singing at night. The difference between estimated repertoires from singing while associating with a female and while engaged in male-male interactions, territorial maintenance, or night singing was statistically significant (see Table 4A).

The mean and standard error of the estimated repertoire size changed during different social situations (Table 3). The mean repertoire size estimates occurring in situations involving the female (labeled F) were larger than estimates derived from singing during other situations. The only situation involving a female that did not produce a large estimate was when a male sang near a border in the presence of his mate. At this time a male's attention (and therefore his singing pattern) probably is directed toward the neighboring male, and the fact that his mate is present is inconsequential. Tukey's studentized range test did not reveal significant differences in repertoire size among the social situations.

Several dichotomies were analyzed by comparing one relatively specific grouping of categories against the sum of observations in all remaining categories for each male in both years. In all comparisons night singing was ex-

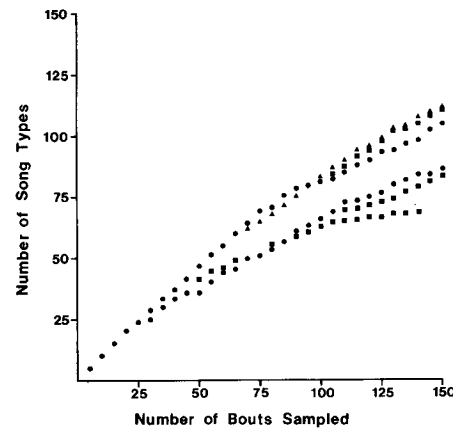


Fig. 3. Examples of exponential curves used to estimate repertoire size in different social situations. The top three curves occurred while males were associating with their mates: male B (▲), 18 April 1980, estimated repertoire size = 256; male A (■), 3 April 1981, 234; and male C (●), 26 March 1980, 197. The bottom three curves, in descending order, represent male C (●), 1 April 1981, patrolling, 120; and male A (■), 16 July 1980, countering session, 94, and 30 July 1980, singing at night, 94.

TABLE 4. Mean and standard error of the estimated repertoire size calculated for 4 males during situational dichotomies.\* The number of estimates used is given in parentheses.

| Individual   | Situation   | Estimated repertoire size |       |     |        |       |       |
|--|-------------|---------------------------|-------|-----|--------|-------|-------|
|  |             | 1980                      |       |     | 1981   |       |       |
|  |             | Mean                      | SE    |     | Mean   | SE    |       |
| <b>A. Associating with the female vs. other situations</b>     |             |                           |       |     |        |       |       |
| A  | Near female | 163.87                    | 48.34 | (5) | 202.38 | 24.73 | (12)  |
|  | Other       | 132.87                    | 31.52 | (9) | 181.51 | 22.17 | (7)   |
| B  | Near female | 174.33                    | 28.80 | (6) | 264.74 | 57.49 | (5) * |
|  | Other       | 137.04                    | 40.68 | (4) | 97.00  | 27.09 | (4)   |
| C  | Near female | 237.13                    | 23.07 | (3) | 111.21 | 11.32 | (3)   |
|  | Other       | 151.08                    | 18.14 | (2) |        |       |       |
| D  | Near female |                           |       |     | 228.98 |       | (1)   |
|  | Other       | 84.46                     | 31.59 | (2) | 143.15 | 44.39 | (2)   |
| <b>B. Patrolling and countering (PAC) vs. other situations</b> |             |                           |       |     |        |       |       |
| A  | PAC         | 93.39                     | 9.77  | (6) | 168.38 | 29.10 | (5)   |
|  | Other       | 181.85                    | 40.45 | (8) | 204.09 | 21.18 | (14)  |
| B  | PAC         | 169.04                    | 43.21 | (3) | 103.21 | 39.14 | (2)   |
|  | Other       | 155.29                    | 29.47 | (7) | 215.04 | 52.31 | (7)   |
| C  | PAC         | 132.93                    |       | (1) | 120.53 |       | (1)   |
|  | Other       | 220.15                    | 23.54 | (4) | 106.54 | 17.86 | (2)   |
| D  | PAC         |                           |       |     |        |       |       |
|  | Other       | 84.46                     | 31.59 | (2) | 171.76 | 38.41 | (3)   |

\* \* =  $P < 0.05$ .

cluded because it could not be assigned unequivocally to either category. The results of two analyses (Table 4) showed that males associated with their mates sang in a fashion that gave larger repertoire size estimates compared with song presented during other situations in all six possible comparisons (Table 4A;  $P < 0.05$ ). One comparison, male B in 1981, was significant by itself. Statistical significance was not achieved for the other males because of small sample sizes and overall variation in the estimate (some of the estimates were based on fewer than 75 consecutive song types). Because repertoire size estimates did not differ among males or between years, males and years were combined. The repertoire size estimate was significantly larger ( $F = 7.92$ ,  $df = 1$ ,  $P < 0.01$ ) when males were associated with their mates (196.90) than during other situations (138.66).

When males were countersinging, patrolling, or near the established border (territorial maintenance), they presented their repertoire in a manner that produced smaller repertoire size estimates compared with song performed during all other situations (Table 4B). When the results for the males were combined, the estimated repertoire size was significantly smaller ( $F = 5.09$ ,  $df = 1$ ,  $P < 0.05$ ) during situations involving territorial maintenance (131.62) than during other situations (184.73). Statistical significance was not achieved for any individual male in either year. Four out of six possible comparisons ( $P > 0.10$ ) were as expected (Table 4B). The results were the same when only the most accurate estimates (samples of greater than 100 consecutive song types) were used. In the third dichotomy nest-associated situations were not significantly different ( $F = 0.71$ ,  $df = 1$ ,  $P > 0.10$ ) from all other situations. However, the mean estimate was larger for the nest-associated situations (186.7 vs. 165.0 song types).

#### DISCUSSION

Before attempting to weigh the relative importance of the various hypotheses on the evolution of the singing behavior of individuals in a particular species, it is necessary to describe accurately the repertoire size of individuals. This is difficult in species in which individuals have extremely large repertoires, such as Northern Mockingbirds. Not only is it in-

trinsically difficult to estimate large repertoires, but many aspects of the individual's social behavior must be controlled for if accurate and comparable estimates are to be obtained.

I used two methods to describe the vocal repertoire size of four male mockingbirds over a 2-yr period. One method, which recorded the number of distinct song types uttered during a breeding season, consistently produced larger estimates. Typically, in well-analyzed birds, repertoires contained a minimum of 200 distinct song types. Often, over 300 distinct song types were obtained for a male in a given breeding season. This method was sensitive to sampling effort. In addition, it probably overestimated the effective repertoire (that measured by females or other males, if they do at all) by accumulating song types that were performed very rarely. To obtain this repertoire size estimate would require females or other males to invest an inordinately large amount of time sampling singing behavior and to have the ability to identify and remember a large number of song types, often hearing them only once. Both of these characteristics are hard to envision evolving and therefore I feel are not likely to occur.

The second method, described by Wildenthal (1965), derives estimates of the repertoire size by fitting an exponential curve to a cumulative plot of distinct song types as a function of consecutive bouts sampled. The resulting asymptote can be used as an estimate of repertoire size. Fewer bouts need to be sampled for this method. The manner of presentation of the song repertoire can influence the estimate. If an individual avoids repeating a bout of a particular song type, a larger estimate will result, especially in contrast to an estimate derived from singing in which bouts of one song type are alternated with a few other song types. It appears that males, by avoiding rapid recurrence of song types, present their repertoire in a manner that results in large estimates of repertoire size. I feel this estimate is more realistic biologically because it requires sampling a shorter sequence of singing (i.e. can be sampled rapidly by females and other males) and can be influenced, and therefore controlled to some degree, by the singer's manner of presentation. For example, males sing in a fashion that produces the largest repertoire size estimates when they are associating with females. This is

consistent with the notion that sexual selection may be involved in the evolution of large repertoires (Kroodsmas 1976; Catchpole 1980; Yasukawa et al. 1980; McGregor et al. 1981; Searcy and Marler 1981, 1984; Kroodsmas and Canady 1985).

The estimation procedure consistently produced smaller repertoire size estimates than did intensive sampling. The mean repertoire size estimate calculated from several singing sessions ranged from 100 to 200 song types. Individual males could not be distinguished statistically. Male rankings differed between years (male A ranked third in 1980 but first in 1981, male B ranked second in both years, male C ranked first in 1980 but last in 1981, and male D ranked fourth in 1980 and third in 1981). This variation in rank can be attributed in part to the fact that estimates will differ depending on the social situation of males when singing. If birds are not sampled in similar social situations, a very likely occurrence, then repertoire size estimates are not comparable. Therefore, when reporting repertoire size estimates it is important to include social situations. Borror (1981) alluded to a similar problem in describing repertoire curves that leveled off but abruptly rose a second or even a third time. The additional rises coincided with the beginning of playback experiments. These playbacks might simulate a change in the social situation.

The difficulties in estimating repertoire size in species with large repertoires should be a major concern when attempting to correlate repertoire size with reproductive success. I feel Howard's (1974) attempt was critically flawed in his estimates of both repertoire size and territory quality in Northern Mockingbirds. To estimate the repertoire of an individual by inspecting 100 spectrograms is inappropriate because repertoire size estimates vary unpredictably, often severely, when samples of less than 125-150 consecutive song types are used. To use only one estimate for each bird is also risky, especially when this single estimate will be used to rank males, because repertoire presentation varies through the breeding season and among social situations (Derrickson 1985, MS). Howard compared males in territory quality, which he estimated from only five sweep samples taken on two consecutive days, again an inadequate procedure. His results (Howard 1974), while possibly correct, should be inter-

preted cautiously. In 1980 mean estimated repertoire size of the four males was associated with minimum known age, pairing date, and number of young fledged. No such relationship existed in 1981. Two factors might have attributed to this lack of association in 1981. First, male C died early in 1981 after having been the most successful male in the study population in 1980. Second, few young fledged in 1981 [only 3 young fledged successfully (1 nest) from 7 pairs (many with multiple nesting attempts)], making the comparison between estimated repertoire size and number of young fledged impossible.

Repertoire size estimates increased between 1980 and 1981 for three of four males, but not significantly. These results appear to be consistent with the general impression that repertoire size in various species increases with age (Rice and Thompson 1968, Marler et al. 1972, Howard 1974, Nottebohm and Nottebohm 1978, Yasukawa et al. 1980).

Attempts to understand the neural pathways responsible for or the proportion of the brain involved in song learning (Nottebohm and Nottebohm 1978) or song production (see review by Arnold 1982) in species with large repertoires requires accurate estimates of the repertoire size of individual males (see Kroodsmas and Canady 1985 for one possible solution). That social factors, seasonal shifts in presentation, and sheer size make it difficult to estimate repertoire size in species such as the mockingbird is troublesome. It will be difficult to understand the neural pathways responsible for song learning without accurate estimates of the size of repertoires of individual males.

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