

SONG REPERTOIRES AND THE SINGING BEHAVIOR OF MALE NORTHERN CARDINALS

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ABSTRACT.—The singing behavior of male Northern Cardinals (*Cardinalis cardinalis*) was examined to determine how singing is used in communication between individuals and, specifically, to determine if different song types convey different information. The mean number of songs per observation period, mean number of songs per bout, and mean number of notes per song were all highest during the pre-nesting and nest-building periods. The higher singing rates and longer songs observed during these periods may play a role in mate attraction/stimulation, and reduce trespassing by conspecific males. Both the mean number of songs per bout and the mean number of notes per song varied significantly among males, perhaps reflecting differences in male quality. During interactions with conspecific males, the mean number of songs per bout decreased while the mean number of notes per song increased. Males tended to utter songs with a greater number of different note types during interactions with conspecific males and females. Thus, variation in several song parameters apparently was used to convey information concerning motivation. Although some significant associations between song types and contexts were observed, all such associations were imperfect. Thus, some song types may be used in a graded form of communication, correlated with, but not restricted to, particular contexts. Most song types, however, appeared to be used randomly with respect to context. Received 16 Nov. 1987, accepted 15 May 1988.

Passerine song may advertise specific and individual identity (Becker 1982, Falls 1982) and may also provide information concerning motivation (Catchpole 1973) and male quality (Lambrechts and Dhondt 1986, 1987). As noted by Becker (1982), information may also be conveyed through changes in song length, amplitude, frequency, or complexity. Additional information may be conveyed through the use of different themes or song types. For example, diverse repertoires might reduce habituation, misrepresent territorial density, confuse territorial neighbors, attract or stimulate mates, or indicate the singer's capabilities for defending their territories (Schroeder and Wiley 1983). It is also possible that certain themes or song types might convey more specific information. Baptista (1978), for example, noted that Cuban Grassquits (*Tiaris canora*) use one song type for aggressive interactions and another for intersexual interactions. Different song types have been reported to be associated with certain contexts in other species as well (Smith 1959, Smith et al. 1978, Gaddis 1983, Schroeder and Wiley 1983, Johnson 1987).

Several aspects of the singing behavior of Northern Cardinals (*Cardinalis cardinalis*) have been examined. The songs of Northern Cardinals

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have been found to vary geographically (Lemon 1966) and males respond differently to playback of songs from different areas (Lemon 1967). Male cardinals generally have song repertoires of 8 to 12 song types, many of which are shared with neighboring males (Lemon 1968). When singing, male cardinals utter a series or bout of one song type, followed by a series of another type. When neighboring males sing simultaneously, they often use the same song type (Lemon 1968). Such matching may permit a male to direct a "message" to a particular individual, and both song length and bout length may provide additional information concerning the motivation of a singing cardinal (Lemon 1968, Gottfried and Gottfried 1978). Conner et al. (1986) reported a possible relationship between song length and nesting success in Northern Cardinals, with more successful males using songs that were less complex and shorter. Although these studies have provided much information about the singing behavior of Northern Cardinals, questions still remain concerning the significance of song repertoires in this species. The objective of this study was to examine how singing is used in communication between male Northern Cardinals and, specifically, to determine if different song types convey different types of information.

MATERIALS AND METHODS

Observations of five male Northern Cardinals located on contiguous territories were made from 26 February through 6 September 1985 at the Central Kentucky Wildlife Management Area, located 17 km SSE of Richmond, Madison County, Kentucky. Each male was observed approximately once every 9 days, thus averaging about 20 times throughout the study. All males under observation were captured in mist nets and marked with colored leg bands and colored plastic tape attached to the rectrices (Ritchison 1984). Observation periods were two h in duration and began at or shortly after sunrise. I attempted to record on tape all bouts of song. Whether recorded or not, for each bout uttered by the focal male I noted the date and nesting stage. The nesting period was divided into six stages: pre-nesting, nest building, incubating, brooding (female spending most of her time at the nest and male feeding female and young), post-brooding and early post-fledging (both adults feeding young), and late post-fledging (male feeding fledged young and female beginning another nesting attempt). I also recorded song types (Figs. 1, 2), the number of songs per bout and the number of notes per song. These data were generally obtained by reviewing field recordings. Although each song type consisted of unique note types, the number of such notes per song was variable. For example, song type I consisted of repetitions of the same note type. Although type I songs sometimes consisted of seven such notes (as in Fig. 2), the number of notes in type I songs (and other types of songs) was variable.

Bouts were defined as a series of songs of the same type. Although such bouts were often separated in time from each other by intervals that were significantly longer than the intervals between songs within a bout, males sometimes uttered bouts in rapid succession. In such cases, the length of time between successive bouts was similar to the length of time between songs in a bout.

I further noted whether or not the focal male was within 25 m of the territory boundary, and any interaction with other males. There were four categories of interactions: spontaneous

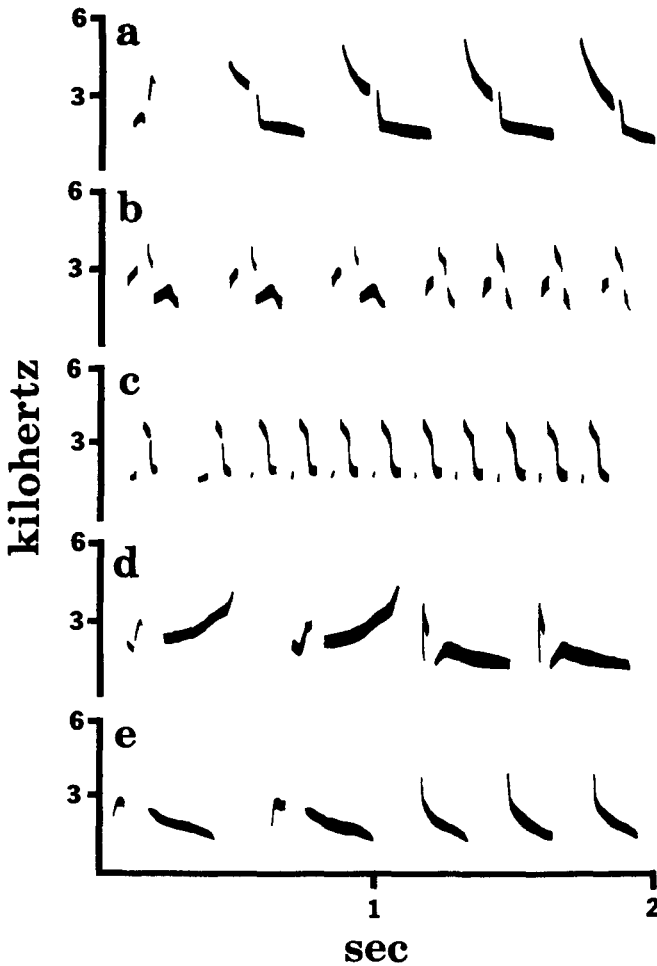


FIG. 1. Song types used by male Northern Cardinals (a-e).

advertising (no other males singing), distant exchange (countersinging with another male at a distance of more than 25 m), distant exchange and matching (countersinging and both males using the same song type), and close exchange (countersinging with another male at a distance of less than 25 m). I also noted the location of females and categorized them as: very close (within 5 m), close (within 25 m), or distant (not within 25 m). Finally, I noted whether or not the focal male was within 10 m of the nest or young.

Each of the five males under observation used the same nine song types. Although males exhibited some interindividual variation (Fig. 3), all song types were easily identified in each male's repertoire. With practice, each song type could be recognized by ear in the field. A Kay Elemetric Sonagraph (Model 6061A) at wide-band settings was used to verify identification of song types made in the field. Recordings were made with a Uher 4000 Report

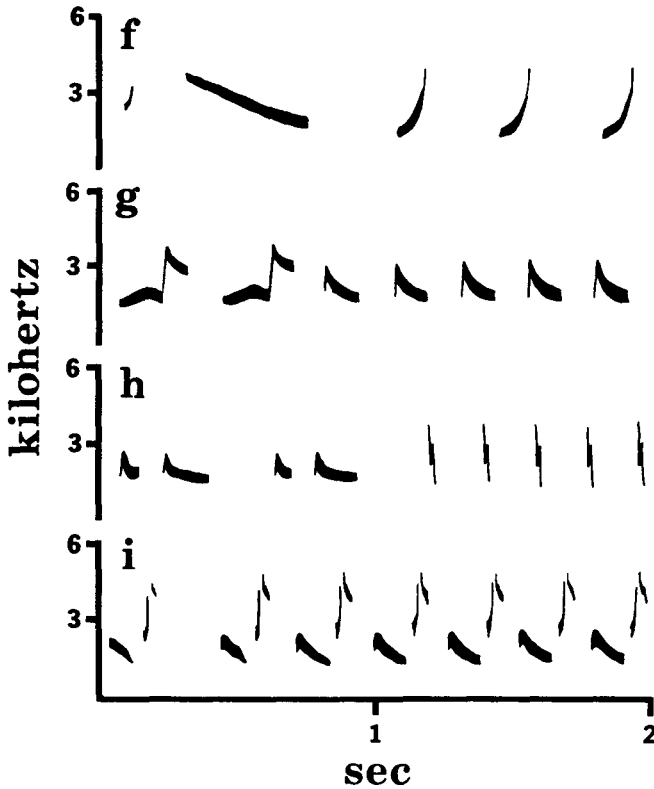


FIG. 2. Song types used by male Northern Cardinals (f-i).

Monitor tape recorder with a Dan Gibson parabolic reflector and microphone. All analyses were performed using procedures found in the Statistical Analysis Systems Guides (SAS Institute 1985). Differences in number of notes per song and number of songs per bout were analyzed for variance (GLM procedure) and post hoc comparisons were made using the Student-Newman-Keuls (SNK) test. Contingency tables were constructed by tallying each song type's occurrence in song bouts associated with specific behavioral contexts. Chi-square tests were used to test for non-random distributions. Sample sizes for individual males were sometimes too small to permit statistical testing and, therefore, data concerning song types and context for all males were pooled. In such cases, it was necessary to assume that all males in the population used song types similarly with respect to context.

RESULTS

Singing rates. — Five male Northern Cardinals were observed for a total of 206 h (103 days) from 26 February through 6 September and these males uttered an average of 140.8 ± 10.3 [SE] songs per two hour observation period. Although not significant, the mean number of songs per

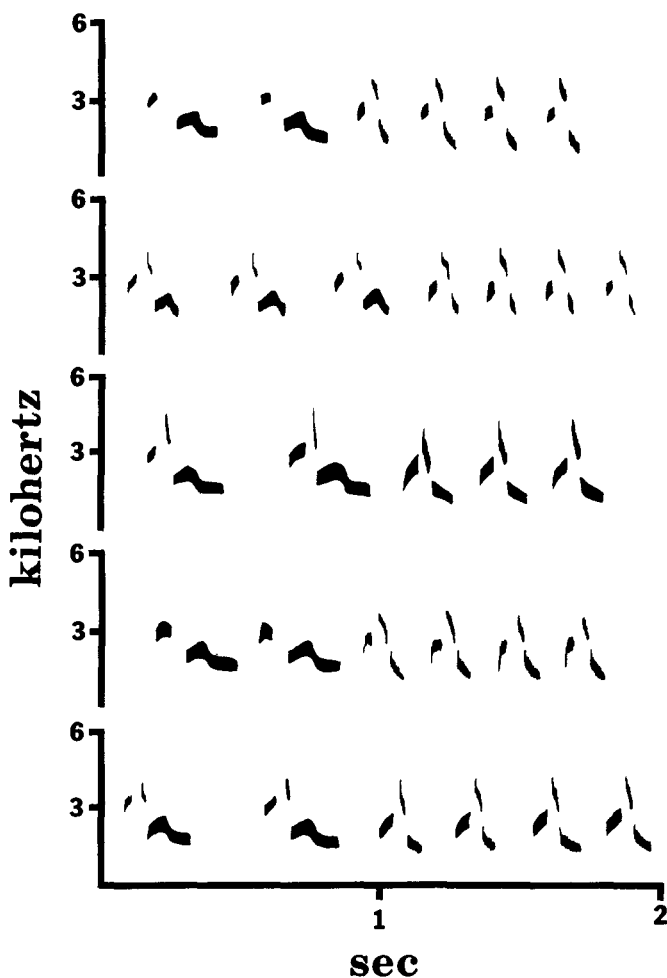


FIG. 3. Interindividual variation in song type B of five male Northern Cardinals.

observation period did vary by month ($F = 2.15$, $P = 0.0545$), with singing rates highest from February through April (Fig. 4). Singing rates did vary significantly by nesting stage ($F = 2.54$, $P = 0.0332$), with rates highest during the pre-nesting and nest-building periods. Although singing rates declined during the brooding and post-brooding/early post-fledging periods, singing increased again during the late post-fledging period as females initiated new nests (Fig. 5).

Number of notes per song, all song types combined. — The mean number of notes per song was 6.74 ± 0.14 ($N = 14,629$ songs). A significant

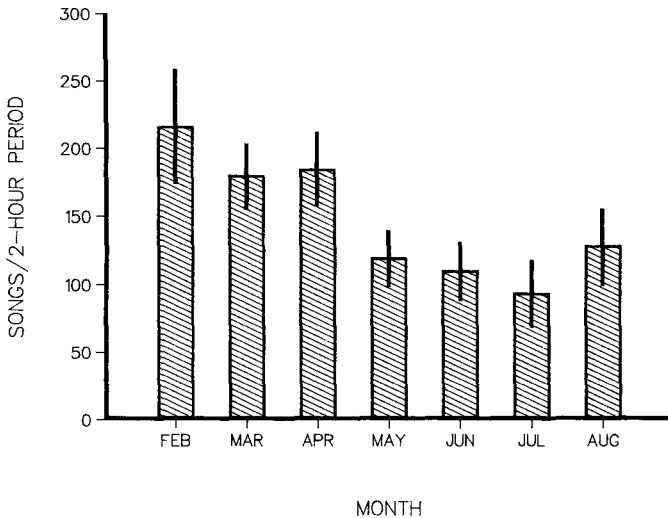


FIG. 4. Mean [±SE] number of songs per two-hour observation period by month.

difference was observed in the mean number of notes per song by month ($F = 16.11$, $P < 0.001$), with more notes per song in February, March, April, and August ($P < 0.05$, SNK test; Fig. 6). The mean number of notes per song also varied significantly with nesting stage ($F = 9.34$, $P < 0.001$), with a greater number of notes per song during the pre-nesting and nest-building periods ($P < 0.05$, SNK test; Fig. 7).

Although each song type exhibited some variation in number of notes per song, each type was usually composed of the same type(s) of notes (Figs. 1, 2). However, males sometimes uttered songs with extra notes at the end, usually a low frequency trill. Bouts that included songs with these extra notes were more common in February, March, and April ($\chi^2 = 28.26$, $df = 6$, $P < 0.001$). Such songs were also uttered more often during the pre-nesting and nest-building periods ($\chi^2 = 23.74$, $df = 5$, $P < 0.001$).

Number of notes per song, individual song types.—The nine song types differed significantly in mean number of notes per song ($F = 38.49$, $P < 0.001$), with song type C consisting of significantly more notes and song types D, E, and F of significantly fewer notes ($P < 0.05$, SNK test). Song types C ($F = 4.38$, $P = 0.009$), D ($F = 6.71$, $P < 0.001$) and I ($F = 9.67$, $P < 0.001$) differed significantly in mean number of notes by month, with each consisting of significantly more notes per song in February ($P < 0.05$, SNK test). Song type F also differed significantly by month ($F = 4.10$, $P = 0.012$), with more notes per song in April than July ($P < 0.05$, SNK test). Four of the nine song types exhibited significant differences in

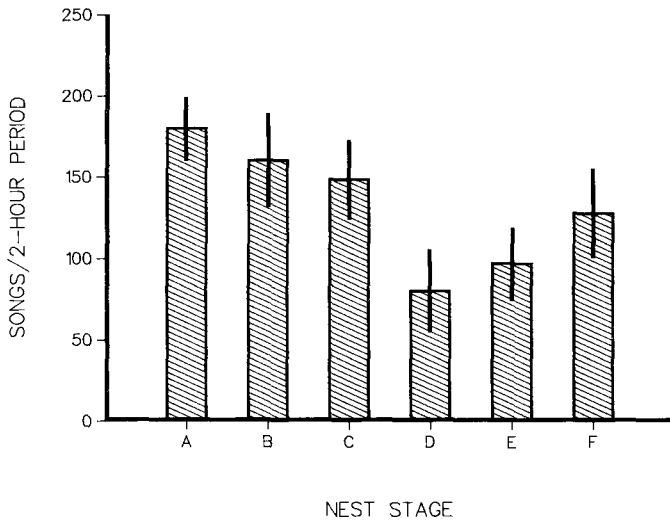


FIG. 5. Mean [\pm SE] number of songs per two-hour observation period by nest stage. (A = pre-nesting, B = nest building, C = incubating, D = brooding, E = post-brooding and early post-fledging, F = late post-fledging.)

mean notes per song by nesting stage, F ($F = 2.42$, $P = 0.0419$), G ($F = 2.98$, $P = 0.0156$), H ($F = 2.40$, $P = 0.0456$), and I ($F = 3.07$, $P = 0.0142$). For each of these four song types, the mean number of notes per song increased during the late post-fledging period after declining to a low during the preceding period(s) (Fig. 8).

Number of bouts and songs per bout.—The mean number of bouts per observation period was 5.64 ± 0.27 . No significant differences were observed in mean number of bouts per observation period on a weekly ($F = 0.73$, $P = 0.818$), biweekly ($F = 1.17$, $P = 0.315$), or monthly ($F = 1.94$, $P = 0.082$) basis. No significant differences were noted in mean number of bouts per observation period during the different stages of the nesting cycle ($F = 1.19$, $P = 0.319$). The mean number of songs per bout was 18.49 ± 0.68 ($N = 790$ bouts), with no significant differences among the nine song types ($F = 0.52$, $P = 0.844$). Significant differences were observed in the number of songs per bout by month ($F = 4.71$, $P < 0.001$), with bouts typically consisting of more songs in March and April ($P < 0.05$, SNK test; Fig. 6). The mean number of songs per bout also varied with nesting stage ($F = 3.66$, $P < 0.003$), with significantly fewer songs per bout during the brooding and post-brooding/early post-fledging periods ($P < 0.05$, SNK test; Fig. 7).

Number of song types.—The mean number of different song types used

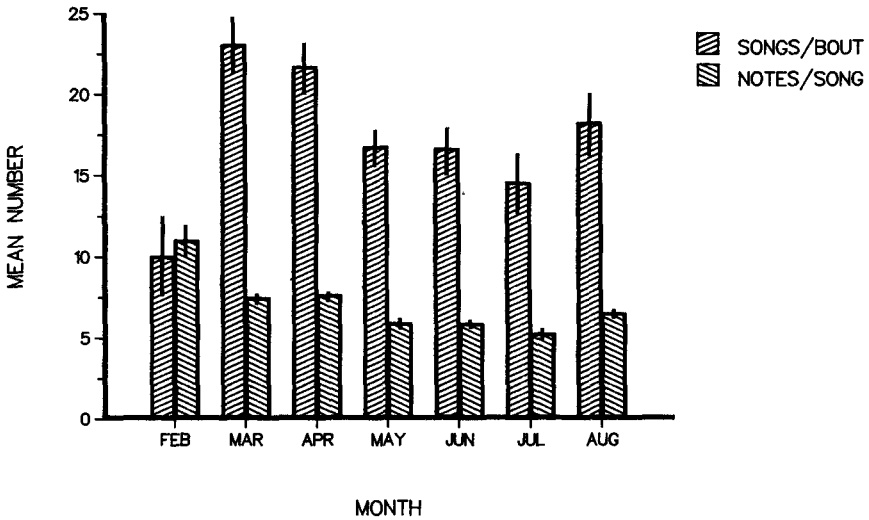


FIG. 6. Mean [\pm SE] number of notes per song and songs per bout by month.

by the males per observation period was 4.41 ± 0.18 . No significant differences were observed in the mean number of song types used per observation period on a weekly ($F = 0.81$, $P = 0.719$), biweekly ($F = 1.22$, $P = 0.281$), or monthly ($F = 1.66$, $P = 0.139$) basis. Similarly, no significant relationship was noted between the mean number of song types used per observation period and nesting stage ($F = 1.50$, $P = 0.197$).

Individual variation, songs and bouts.—Individual males differed significantly both in mean number of songs ($F = 5.05$, $P < 0.001$) and mean number of bouts ($F = 3.45$, $P < 0.05$) per observation period. Males also differed significantly in the mean number of notes per song ($F = 26.62$, $P < 0.001$; Fig. 9) and the mean number of songs per bout ($F = 6.88$, $P < 0.001$), with one male uttering significantly fewer songs per bout than the other four males ($P < 0.05$, SNK test; Fig. 9). Males also differed in the extent to which they uttered songs with extra notes ($\chi^2 = 24.76$, $df = 4$, $P < 0.0001$), with the percentage of bouts including such songs ranging from 2.8 to 16.8%. Finally, males differed significantly in the mean number of song types used per observation period ($F = 5.34$, $P < 0.0006$), ranging from 3.5 to 5.6.

Notes per song, variation with context.—As the level of interaction with other males increased, the number of notes per song also increased ($F = 18.42$, $P < 0.0001$; Fig. 10). Although songs consisted of the greatest number of notes during close exchanges with other males ($P < 0.05$), males used songs with more notes when matching than during sponta-

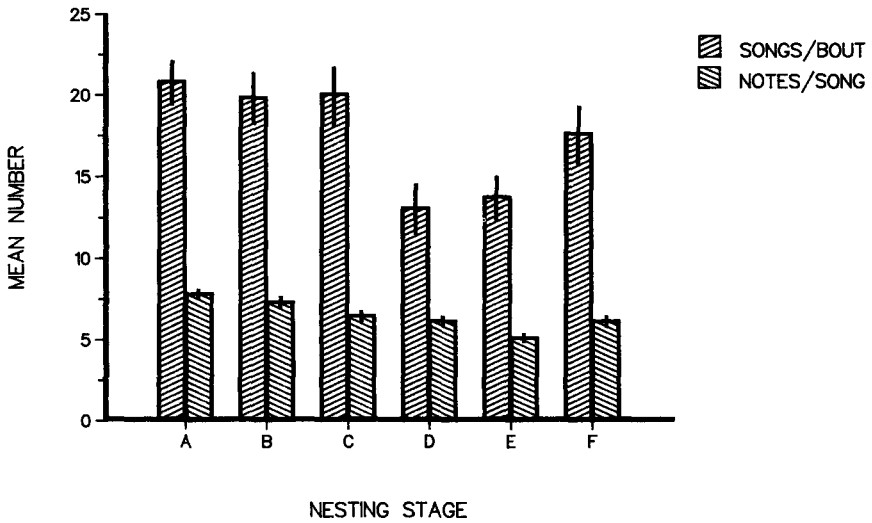


FIG. 7. Mean [\pm SE] number of notes per song and songs per bout by nest stage (see Fig. 4 for meaning of letters).

neous advertising ($P < 0.05$, SNK tests). The number of notes per song also differed with location of the young ($F = 8.43$, $P < 0.005$) and location of the nest ($F = 12.84$, $P < 0.0005$). Males uttered songs with fewer notes when within 10 m of the young or the nest ($P < 0.05$ in both cases, SNK

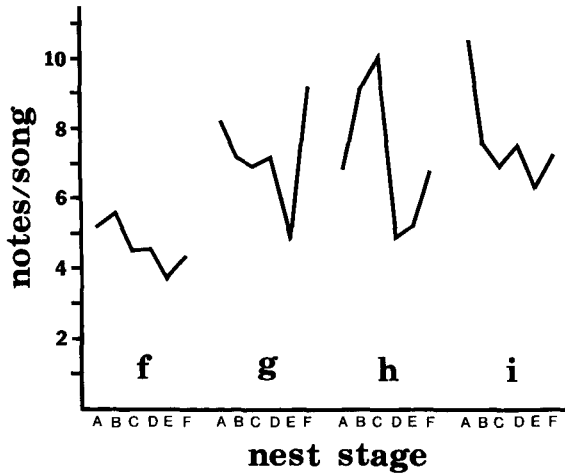


FIG. 8. Mean number of notes per song during different nest stages for song types F, G, H, and I (see Fig. 5 for explanation of nest stage categories).

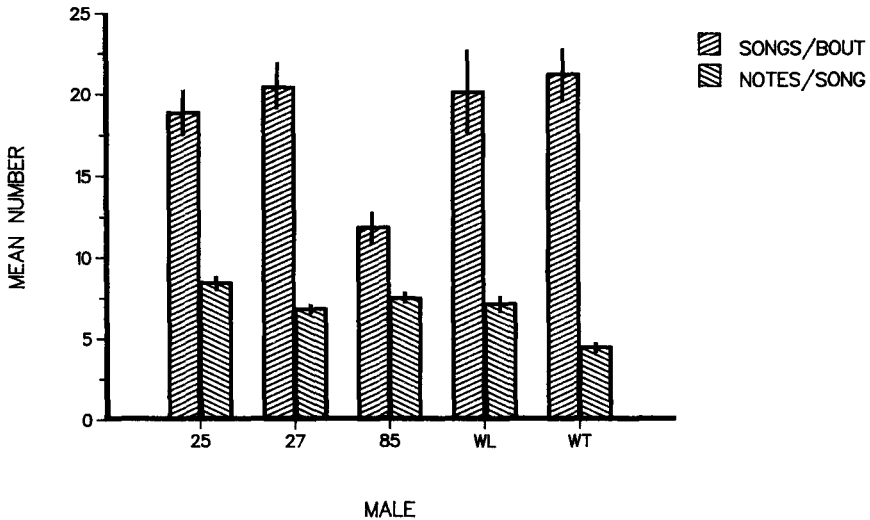


FIG. 9. Mean [\pm SE] number of notes per song and songs per bout for individual males.

tests). No significant relationship was noted between mean number of notes per song and either the location of the male in the territory ($F = 1.11$, $P = 0.290$) or the location of the female ($F = 2.45$, $P = 0.087$).

Songs with extra notes were almost always uttered during close exchanges with either males ($\chi^2 = 180.33$, $df = 3$, $P < 0.0001$) or females ($\chi^2 = 119.49$, $df = 2$, $P < 0.0001$). Such songs were uttered significantly less often when males were within 10 m of the nest ($\chi^2 = 3.94$, $df = 1$, $P < 0.05$). No significant relationship was observed between the use of songs with extra notes and either location in the territory ($\chi^2 = 0.04$, $df = 1$, $P = 0.838$) or location of the young ($\chi^2 = 0.01$, $df = 1$, $P = 0.991$).

Notes per song, variation with context among song types.—Most song types exhibited an increase in mean number of notes per song with increasing level of interaction with other males (Fig. 11). However, differences were significant only for song types C ($F = 5.86$, $P = 0.0013$), F ($F = 3.72$, $P = 0.0281$), G ($F = 6.72$, $P = 0.0004$), and I ($F = 5.37$, $P = 0.0021$). Only song types F ($F = 7.93$, $P = 0.0082$), and G ($F = 4.78$, $P = 0.0408$) differed significantly with location of the young, with both consisting of fewer notes per song when uttered within 10 m of the young. Although all song types consisted of fewer notes per song when uttered within 10 m of the nest, only song types E ($F = 6.89$, $P = 0.0127$) and G ($F = 7.24$, $P = 0.0096$) consisted of significantly fewer notes per song. No song type differed significantly in mean number of notes per song with either location in territory or location of mate.

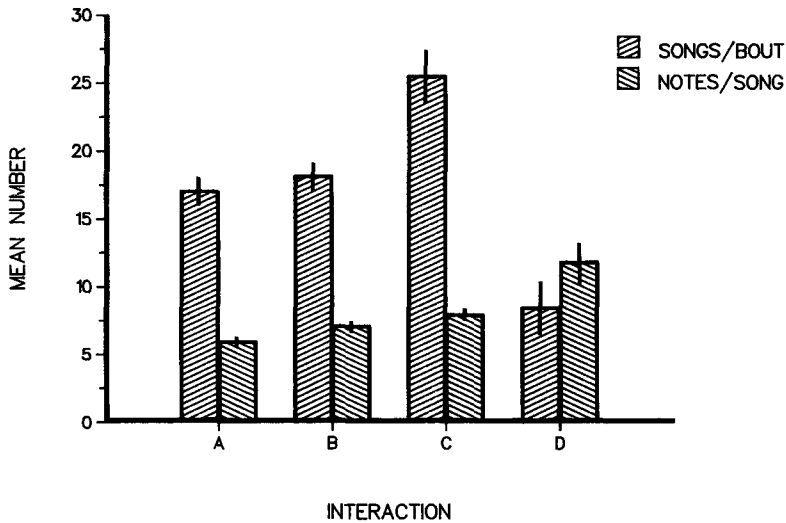


FIG. 10. Mean \pm SE number of notes per song and songs per bout during interactions with other males. (A = spontaneous advertising, B = distant exchange, C = distant exchange and matching, D = close exchange.)

Songs per bout, variation with context.—The mean number of songs per bout varied with the level of interaction with conspecific males ($F = 7.16$, $P < 0.001$), with males uttering fewer songs per bout during close exchanges ($P < 0.05$, SNK test; Fig. 10). No significant relationships were observed between the number of songs per bout and location in the territory ($F = 0.01$, $P = 0.981$), location of females ($F = 1.83$, $P = 0.161$), location of the young ($F = 0.88$, $P = 0.351$), or location of the nest ($F = 1.30$, $P = 0.254$).

Song types.—Individual males differed significantly in use of the nine song types ($\chi^2 = 54.97$, $df = 32$, $P = 0.007$). One male uttered more bouts of song type B than expected (37 vs 23.7) and fewer bouts of song type H (5 vs 16.2). A second male uttered more bouts of song type G than expected (33 vs 21.4), while a third uttered more bouts of song type H than expected (31 vs 20.6). For all males combined, significant nonrandom use by month was observed ($\chi^2 = 70.93$, $df = 48$, $P = 0.017$) for only two song types. Song type A was used less than expected in May while song type G was used less than expected in April and July and more than expected in May and June. No significant relationship was noted between song type and nesting stage ($\chi^2 = 38.94$, $df = 40$, $P = 0.518$).

Song types and behavioral context, all males combined.—Although the nine song types were used in a nonrandom manner during interactions

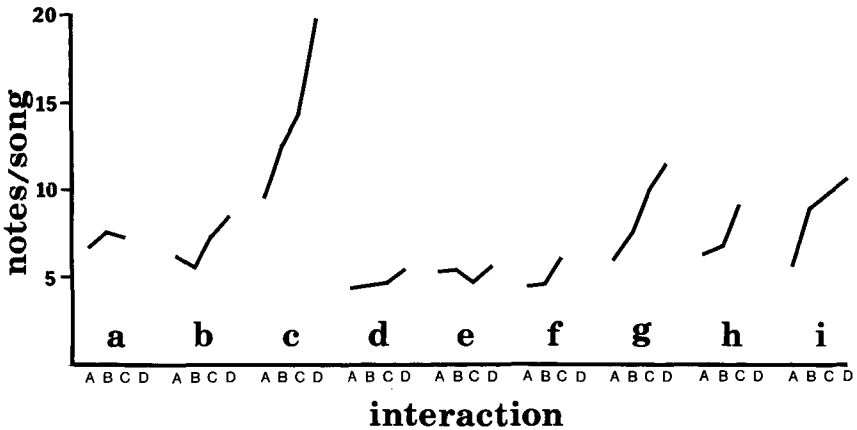


FIG. 11. Mean number of notes per song during interactions with other males for song types A–I (see Fig. 10 for explanation of interaction categories). Song types A, F, and H were never used during close exchanges with other males (category D).

with other males ($\chi^2 = 36.56$, $df = 24$, $P = 0.048$), further analysis revealed significant nonrandom associations for only three song types. Bouts of song type B were used more than expected (58 vs 48.6) while bouts of song types C and I were uttered less than expected during spontaneous advertising (26 vs 32.4 and 26 vs 35, respectively). Further, nine of 16 bouts of song uttered during close exchanges with other males consisted of either song type C or I (4 and 5 bouts, respectively). Nonrandom use of song types was also noted during interactions with females ($\chi^2 = 32.09$, $df = 16$, $P = 0.01$), with males using song type H more than expected (14 vs 5.6) when females were within 5 m.

Song types and behavioral context, individual males.—Sample sizes for individual males were large enough to permit statistical testing for nonrandom use of song types with respect to location in the territory, location of fledged young, and location relative to the nest, respectively. In each of these contexts the use of different song types was found to be random.

Although sample sizes for individuals were too small to test for significance, all males exhibited a similar pattern during interactions with other males. That is, all five males used song type B more than expected and song types C and I less than expected during spontaneous advertising. Further, four males uttered bouts of song during close interactions with other males and all used either song type C or I during such encounters. Two of these males were each involved in two such encounters and song type I was used in each case. The other two males also used either song

type C or I during close interactions with other males, although not exclusively (3 of 7 bouts for one male and 2 of 5 for the other).

Sample sizes for individual males were also too small to test for possible associations between song types and interactions with females. As noted above, song type H was significantly associated with very close interactions with females for all males combined. However, one male accounted for seven of the 14 bouts of this song type uttered during such interactions. Two additional males used several song types during such interactions, including song type H (4 of 9 and 3 of 11 bouts, respectively). The two remaining males uttered a total of 26 bouts during such interactions (10 and 16, respectively) and never used song type H.

Order of and intervals between bouts.—Male cardinals sometimes uttered a series of bouts in rapid succession and the nine song types differed significantly in the order in which they were used in such series ($F = 4.07$, $P = 0.001$). Males often used either song type F (mean order = 1.16 ± 0.06) or A (mean order = 1.27 ± 0.10) initially while song types D (mean order = 2.18 ± 0.26) and C (mean order = 2.22 ± 0.33) were typically used later in such series.

Position changes.—The five male Northern Cardinals changed perches while singing on 387 occasions. In most cases (300 or 77.5%) males switched to a different song type after changing positions. This tendency to switch song types after a position change was noted throughout the study, with no differences noted on a monthly basis ($\chi^2 = 8.35$, $df = 6$, $P > 0.1$).

DISCUSSION

Singing behavior, variation over time.—Singing rates of males have been found to vary during the breeding season in many passerine species (Catchpole 1982), and male Northern Cardinals are no exception. Although male cardinals sang throughout the present study, singing rates declined somewhat after April. Kinser (1973) observed that singing by male cardinals was uncommon in July and August in southern Indiana. Much of the variation in singing rates noted in the present study appeared to be related to nesting stage, with rates highest during the pre-nesting, nesting, and incubation periods, much lower during the brooding and post-brooding/early post-fledging periods, and higher during the last post-fledging period.

Cardinals are multibrooded, with one pair sometimes raising three or four broods per year (Laskey 1944, pers. obs.). In addition, cardinals frequently lose nests to predators (pers. obs.). Thus, female cardinals initiate several nesting attempts during a breeding season. The singing

rates of male cardinals in the present study typically increased after a nest was lost to predators or when a female was beginning another nesting attempt after young from the previous nest had fledged. Kinser (1973:76) also reported that singing rates of male cardinals increased "following the departure of a brood or the loss of a nest." Such song cyclicity has been reported in other species, particularly multibrooded species (Slagsvold 1977, Logan 1983). Logan (1983) suggested that a mechanism for resetting the complicated endocrine interactions essential for a normal nesting cycle would be adaptive in multibrooded species subject to considerable predation or nest loss. Thus, the increased singing rates of male cardinals during the period when a female is beginning another nesting attempt may be a means by which the female's reproductive system is reset. It is also possible that higher rates of singing are directed toward conspecific males. When females initiate another nest, other males may seek extra-pair copulations (Birkhead et al. 1987). If so, increased levels of territorial defense (increased rates of singing) by the female's mate may reduce trespassing by conspecific males and help to insure paternity.

Other changes in the singing behavior of male cardinals were also observed. During the pre-nesting period, bouts consisted of significantly more songs, songs typically consisted of a greater number of notes (significantly greater for 4 of 9 song types), and songs with extra notes were more common. Conner et al. (1986) suggested that young male cardinals may use longer, highly complex songs when first establishing a territory. Perhaps all male cardinals use a similar strategy on an annual basis, using longer bouts and longer, more complex songs during the period of territory establishment (pre-nesting period). Once boundaries are established they may put "less effort" into song, resulting in shorter, less complex songs. It is also possible, however, that changes in singing behavior are related to other factors. For example, males may continue to use longer bouts and songs even after territories have been established if, as noted above, trespassing neighbors or other males might attempt to copulate with their mate. The chance of such extra-pair copulations may lead males to maintain high levels of territory defense, including continued "complex" singing. The longer bouts and longer, more complex songs may also play a role in mate attraction (or "stimulation" as just described). Once paired (or once nesting has begun), males may again put less effort into song. The breeding chronology of cardinals suggests that either (or both) the mate guarding or mate attraction/stimulation hypothesis may be correct. Territory boundaries are well established by mid-March or even earlier (Ritchison 1986), yet males in the present study continued to utter more songs per bout, more notes per song, and more songs with extra notes through April. The increased number of songs per bout and number of

notes per song noted during the late post-fledging period when females were initiating new nests further suggests that the "complex" singing of male cardinals may be more important for either (or both) mate attraction/stimulation or mate guarding than in the establishment of territories.

Singing behavior, motivational information.—Changes in singing behavior have been found to convey motivational information in a variety of passerine species (Becker 1982) and this also appeared to be true for male Northern Cardinals in the present study. As the intensity of interaction with other males increased, so did the mean number of notes per song, with a mean of six notes per song during spontaneous advertising and nearly 12 notes per song during close interactions with other males. Similar increases in song length during conflict situations in cardinals have been reported previously. Gottfried and Gottfried (1978) performed playback experiments with male Northern Cardinals and found that the number of notes per song decreased significantly during playback but increased significantly during the post-playback period, with a mean of over 16 notes per song. Similar increases in song length either during conflict situations or after exposure to playback have been reported in the Indigo Bunting (*Passerina cyanea*, Emlen 1972), Black-headed Grosbeak (*Pheucticus melanocephalus*, Ritchison 1983), and Willow Warbler (*Phylloscopus trochilus*, Helb 1973).

As noted above, male cardinals sometimes uttered songs with extra notes at the end. Males often uttered these songs during situations suggesting a high level of excitement, either when other males were within 25 m or females were within 5 m. The extra notes were often harsh, wide-band in structure, and low in frequency and usually included a trill or "growl." It has been suggested that harsh sounds are generally aggressive in nature (Morton 1977, 1982). However, these notes were used in the presence of both males and females, suggesting that they were not purely aggressive in nature. Other authors have reported the use of more complex songs, often in aggressive contexts. For example, Bremond (1968) reported that European Robins (*Erithacus rubecula*) utter songs of greater complexity when they are likely to attack. Lein (1978) observed that Chestnut-sided Warblers (*Dendroica pensylvanica*) use a highly variable song ("jumbled song") only during territorial encounters. Groschupf (1985), on the other hand, reported that male Five-striped Sparrows (*Amphispiza quinquestriata*) used more complex songs in intrasexual contexts. The complex songs of cardinals may simply communicate increased excitement or likelihood of interacting, regardless of sex.

Male Northern Cardinals also appeared to use changes in bout length to provide motivational information. When counter-singing and, especially, when matching neighboring males the mean number of songs per

bout generally increased. Lemon (1968) suggested that matching may permit male cardinals to direct a "message" to a particular individual. An increased number of songs per bout during such interactions may help insure reception of the message by that individual. On the other hand, during close exchanges with males the mean number of songs per bout decreased significantly, with males switching song types more rapidly as the probability of confrontation increased. Lemon (1968) noted similar behavior by male Northern Cardinals. Increased rates of switching during intense territorial encounters have been reported in many other species, including the Plain Titmouse (*Parus inornatus*, Dixon 1969), Chestnut-sided Warbler (Lein 1978), Red-winged Blackbird (*Agelaius phoeniceus*, Smith and Reid 1979), Song Sparrow (*Melospiza melodia*, Kramer and Lemon 1983), and Carolina Wren (*Thryothorus ludovicianus*, Simpson 1985).

Singing behavior, individual variation.—All five male Northern Cardinals used the same nine song types. Extensive sharing of song types by male cardinals has been reported previously (Lemon 1965, 1966). Such sharing means there is little or no variation among male cardinals in the size of their song-type repertoires, providing females with little information about the relative quality of males. However, other characteristics of song could be correlated with male quality. As noted previously, Conner et al. (1986) found that male cardinals exhibited differences in song complexity, and males with less complex songs appeared to hold better quality territories. Female cardinals might perceive these differences in song and use this information to choose a male with a better quality territory. In the present study, the five male cardinals exhibited significant differences in both mean number of songs per bout and mean number of notes per song. As noted previously, variation in these measures appears to provide information concerning motivation, with shorter bouts and longer songs apparently indicating increased excitement or likelihood of interacting. Variation in these measures could also provide information about male quality. A similar correlation has been reported in the Great Tit (*Parus major*). Lambrechts and Dhondt (1986) reported a significant correlation between winter dominance position (a measure of male quality) of male Great Tits and mean song length (number of phrases per song). In the present study, the mean number of notes per song was significantly lower than the population mean for one male cardinal (4.5 vs 6.7). Interestingly, this male was also the last of the five males in the present study to pair with a female. Although these results and those of Conner et al. (1986) are suggestive, studies with additional males are needed to determine if there is a correlation between various measures of song quality and male mating success.

Song types and context. — Few significant associations between song type and context were observed in the present study, and all such associations were imperfect. In other words, all song types were used in several contexts and each context involved the use of most or all song types. Song type B was found to be significantly associated with spontaneous advertising. Further, the mean order of use of this song type in a series of bouts was relatively low, indicating early use in such series. In addition, although not significant, the mean period of silence before bouts of song type B was the longest of any song type. Such spontaneity is a characteristic feature of vocalizations that serve in territorial advertisement (Marler 1968). Although song types C and I were found to be associated with close exchanges between males, only sixteen such exchanges were observed. Further, two of the four males that sang during such exchanges used other song types in addition to song types C and I. For all males combined, song type H was significantly associated with very close interactions with females. However, one male accounted for seven of the 14 bouts of this song type used in such interactions and, further, two of the five males in the present study were not observed to use this song type during very close interactions with females. The use of song types by male cardinals was random with respect to nesting stage, location in the territory, location of fledged young, and location relative to the nest.

Investigators have reported clear contextual associations for different song types in Chestnut-sided Warblers (Lein 1978) and Bridled Titmice (*Parus wollweberi*, Gaddis 1983). However, the association between song types and contexts has proven to be imperfect in most species (Smith et al. 1978, Gaddis 1983, Kramer and Lemon 1983, Derrickson 1987, Johnson 1987). Kramer and Lemon (1983) proposed three possible explanations for such findings: (1) The contexts chosen by an investigator may only approximate the circumstances relevant to the birds in their differential production of song types. (2) Each song type may contain a probability of less than one of encoding a particular message, implying that song types are used in a graded form of communication. (3) The associations may simply be a by-product of other patterns of singing.

Kramer and Lemon (1983) suggested that the observed association between song type and context in Song Sparrows may have been a by-product of the correlation between bout length and context. Lending further support to their conclusion that the observed associations probably had little or no meaning to the birds was the finding that neighboring Song Sparrows shared few song types. Clear associations between certain song types and certain messages would be more likely in species where neighboring individuals share most or all song types (Smith et al. 1978). I found no significant differences among cardinal song types in number

of songs per bout in different contexts. In other words, the mean number of songs per bout changed with certain contexts but such changes were observed for all song types. Thus, the associations between song types and context in cardinals do not appear to be the by-product of cardinal singing patterns. Further, neighboring cardinals share most or all song types (Lemon 1968, this study). Thus, if the contexts I have chosen are in fact relevant to the birds, then perhaps certain cardinal song types (e.g., B, C, and I) are used in a graded form of communication. In other words, these song types may be correlated with, although certainly not restricted to, certain contexts or behaviors. However, most song types in the present study were not significantly associated with particular contexts. This may be the result of inadequate sampling (and thus having to pool data for all males), an imperfect choice of contexts, or, perhaps, some song types simply exhibit no associations. Song types not associated with specific contexts or behaviors could serve other functions, e.g., facilitating vocal interactions with neighbors (Kroodsma 1979), avoiding monotony (Hartshorne 1956, Kroodsma 1978), permitting males to accurately judge the distance of conspecifics that use the same song types (Morton 1982, 1986), or preventing exhaustion that might result from repeating the same song type (Lambrechts and Dhondt 1988). In addition, Johnson (1987) suggested that all or part of an individual's song repertoire may serve no function, being created or maintained simply as a by-product of the song learning process.

Song repertoires and the Beau Geste hypothesis.—The Beau Geste hypothesis (Krebs 1977) provides a mechanism by which repertoires of song types can function in territorial defense, with the use of multiple song types creating the impression of a densely populated area. Such deception would be enhanced if singers would change positions between bouts of different song types. Further, deception should be most pronounced during the period of territory establishment (Schroeder and Wiley 1983). In support of this hypothesis, male Northern Cardinals did exhibit a significant tendency to change perches in conjunction with changes in song type. Simultaneous song and perch changes have been noted in a variety of other species, including Dark-eyed Juncos (*Junco hyemalis*, Williams and MacRoberts 1977), Great Tits (Krebs et al. 1978), Red-winged Blackbirds (Smith and Reid 1979, Yasukawa 1981), and Song Sparrows (Kramer and Lemon 1983). The tendency of male cardinals to switch perches in conjunction with changes in song type was noted throughout the study, with no increase in such behavior during the period of territory establishment. Further, males did not use a greater number of different song types per observation period during the period of territory establishment than during the rest of the breeding season. Thus, the Beau Geste effect

does not appear to provide a complete explanation for the use of song repertoires in the Northern Cardinal. A similar conclusion has been drawn for the Carolina Wren (Morton 1982), Tufted Titmouse (*Parus bicolor*, Schroeder and Wiley 1983), Song Sparrow (Kramer and Lemon 1983), and Red-winged Blackbird (Yasukawa and Searcy 1985).

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MIDWEST RAPTOR MANAGEMENT SYMPOSIUM AND WORKSHOP

The National Wildlife Federation's Institute for Wildlife Research, Illinois Department of Conservation's Division of Natural Heritage, Illinois Chapter of The Wildlife Society, and Max McGraw Wildlife Foundation will host the Midwest Raptor Management Symposium and Workshop, 27 February-1 March 1989, in Chicago, Illinois, at the Allerton Hotel. Participating states include Illinois, Indiana, Iowa, Kansas, Michigan, Minnesota, Missouri, Nebraska, North Dakota, Ohio, South Dakota and Wisconsin.

Day one of the symposium will feature status reports on midwestern raptors, as well as technical papers on survey techniques, population dynamics, raptor depredation, and causes of raptor mortality. On day two, these fact-finding sessions will be followed by panels and workshops on raptor habitat enhancement, restoration efforts and public education. On the final morning of the symposium, brainstorming sessions will provide a unique opportunity for participants to identify issues and develop management recommendations for midwestern raptors.

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