

RELATIONSHIPS AMONG TERRITORY SIZE, HABITAT, SONG, AND NESTING SUCCESS OF NORTHERN CARDINALS

RICHARD N. CONNER,¹ MARY E. ANDERSON,^{2,3} AND
JAMES G. DICKSON¹

¹Wildlife Habitat and Silviculture Laboratory, Southern Forest Experiment Station,
USDA Forest Service, Nacogdoches, Texas 75962 USA, and

²Department of Biology, Stephen F. Austin State University,
Nacogdoches, Texas 75962 USA

ABSTRACT.—We collected data from 30 territories of Northern Cardinals (*Cardinalis cardinalis*) during 3 breeding seasons (1979–1981) in eastern Texas. Territory size was positively correlated with tree height and negatively correlated with the density of foliage at ground level and at 3 m above the ground, and with the density of shrubs. Nesting success was positively correlated with presence of patchy understory foliage and arthropod biomass in territories. Cardinals with low song complexity and shorter songs held better-quality territories and had better nesting success than cardinals with more complex songs. We suspect that young males may use long, complex songs to establish a territory initially, and in subsequent years put less time and effort into song and more into care and defense of young.
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THE functional significance of song in birds is a widely studied phenomenon. In particular, the significance of song repertoires has recently received extensive examination, resulting in many hypotheses. Krebs (1977a) summarized these hypotheses as follows: (1) repertoires enhance individual recognition (Emlen 1971, Brooks and Falls 1975); (2) repertoires are a product of sexual selection (Catchpole 1973, Kroodsma 1977); and (3) repertoires increase success in territorial competition by allowing acquisition of larger (Krebs 1977b) or better-quality (Howard 1974) territories.

Large repertoires could permit matched countersinging among males establishing or defending territories (Lemon 1968, Verner 1975) or reduce habituation of listeners (Hartshorne 1956). Krebs (1977a) suggested a new mechanism (the Beau Geste hypothesis) whereby large song repertoires could be used to create the illusion that a particular habitat area was already saturated with numerous territorial males.

Holding territory size constant, repertoire size of Northern Mockingbirds (*Mimus polyglottos*) in central and western Texas was correlated with measurements of territory quality (Howard 1974). Male mockingbirds with larger

repertoires also had the highest success in excluding other males and attracting females. If males with larger repertoires or some other song characteristic are able to establish and maintain larger or better-quality territories, such males should have a higher nesting success than males with territories of lesser quality. High-quality territories should have a greater availability of food and nest concealment than low-quality territories. Females from an inbred strain of canaries (*Serinus canaria*) exposed to playbacks of males with large repertoires built nests faster and laid larger clutches than did females exposed to small repertoires (Kroodsma 1976).

Female birds may select males on the basis of song quality or select the territory of a male because of the habitat's appearance through mechanisms similar to those by which males may identify habitat quality. If either method was used, pairs in higher-quality habitat (more food and better concealment available) might be expected to produce more eggs or young on the average than pairs in lower-quality territories. Although predation would have a substantial impact on nesting success (Best 1978), vegetation structure or quality may also have an influence on predation and nesting success of birds (Best and Stauffer 1980). Vegetation characteristics around nests were correlated with nesting success of Vesper Sparrows (*Pooecetes gramineus*) in a 1-yr study in West Virginia

³ Present address: Math and Science Division, Bee County College, Beeville, Texas 78102 USA.

TABLE 1. Characteristics of cardinal songs and 100 randomly selected syllables from 30 territories over a 3-yr period in eastern Texas.

Variable code	Description	Mean	SD
Songs			
ASYB	No. of syllables per song	10.45	2.49
DSYB	No. of different syllables per song	1.61	0.23
TRAN	No. of syllable transitions per song	0.62	0.23
SBVS	Total versatility of syllables per song	0.08	0.08
SLGT	Song length (s)	2.78	0.59
ISI	Intersong interval (s)	6.33	1.33
NSGS	No. of songs recorded per bird	311.27	267.87
SBRP	Syllable repertoire per male	15.50	4.52
STRP	Song-type repertoire per male	18.67	8.16
SGVS	Total versatility of song type per male	7.62	2.90
RESB	Residual of syllable repertoire	-0.22	2.76
REST	Residual of song-type repertoire	-0.16	4.26
Syllables			
FMOD	Frequency modulation (degree)	46.20	5.82
FEMP	Frequency emphasized (kHz)	2.20	0.42
HIFR	High frequency (kHz)	4.19	0.58
LOFR	Low frequency (kHz)	1.33	0.24
FRGE	Frequency range (kHz)	2.87	0.56
SYBL	Syllable length (s)	0.24	0.04
ISBI	Intersyllable interval (s)	0.13	0.02
NELM	No. of elements per syllable	2.84	1.26

(Wray and Whitmore 1979). Concealment, nest height, and adult body weight were also significantly related to nesting success in a riparian bird community in Iowa (Best and Stauffer 1980).

We examined relationships of territory size and habitat quality with song characteristics and nesting success of Northern Cardinals (*Cardinalis cardinalis*) in eastern Texas to evaluate associations of song with habitat and nesting success.

METHODS

Study area.—We selected a diverse "edge" stand (15 ha) for the study in a pine (*Pinus* spp.)-hardwood forest 15 km south of Nacogdoches, Texas. Northern Cardinals were studied in this area during three consecutive breeding seasons (1979–1981). Approximately half of the stand was mature forest (18–22 m tall); most of the remainder was a 4-yr-old loblolly pine (*Pinus taeda*) plantation with dense pine and deciduous foliage that was 2–3 m high in 1979. The mature forest and the pine plantation had patchy foliage and ranged from xeric, sandy hilltops to mesic sites along two streams. The streams ran through forested strips (30–50 m wide) in the pine plantation. Several small openings (0.45 ha total) in the mature forest had a ground cover of grasses and forbs. Dominant tree species in upland portions of the mature forest were

shortleaf pine (*P. echinata*), loblolly pine, post oak (*Quercus stellata*), and sweetgum (*Liquidambar styraciflua*). Dominant tree species in the mature forest along the streams were sweetgum, American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), sweetbay (*Magnolia virginiana*), and hickory (*Carya* spp.). Winged sumac (*Rhus copallina*), smooth sumac (*R. glabra*), and sweetgum were dominant in the pine plantation.

Song recording.—We recorded songs of 30 territorial male cardinals from the end of March through the middle of June with a Uher 4000 report IC tape recorder and a 40-cm Dan Gibson Parabolic EPM P-650 electronic microphone. The time span over which we recorded songs enabled us to sample songs of all males throughout all phases of the nesting season. Males were color marked (colored bands and tarsi streamers) for individual identification. To minimize sound distortion, we made most recordings within 8–15 m of males. We did not use playbacks of song to elicit singing behavior. Only males with 89 or more songs recorded were used for analyses ($n = 30$ males).

All field recordings were reviewed at one-quarter tape speed (2.4 cm/s); syllable types (see Lemon 1965) were initially determined and identified at this reduced speed. The different syllable patterns were verified with spectrograms made on a Kay Elemetrics model 7029A Sona-Graph, using the wide band filter setting with a frequency range of 80–8,000 Hz. Information measured included the kinds and numbers of syllables in each song, song length, and intersong interval (Table 1). Song lengths and intervals were

measured to the nearest 0.1 s with an electronic stopwatch.

One hundred syllables sung by each territorial male cardinal were sampled randomly and spectrograms were made of these 3,000 syllables. We made 8 measurements on each syllable: frequency range, frequency modulation, frequency emphasized, highest frequency, lowest frequency, syllable length, number of elements in each syllable, and the following intersyllable interval (after Morton 1975; Table 1). We measured the frequency emphasized at that point in the syllable where most of the energy was focused, as indicated by the darkest portion of each syllable on the spectrograms.

Frequency modulation of syllables was determined geometrically as an angular measurement of the rate of frequency change. Each syllable was divided into four equal segments, with five vertical lines; this provided five possible points of intersection with the syllable. At each point, the angle of inclination was measured in degrees with respect to the horizontal axis. Each angle was recorded as an acute angle, disregarding the quadrant in which it fell. This simplified the data by ignoring the various modes of inflection inherent in cardinal syllables. The five angle measurements were averaged and used as an index of frequency modulation, a measure of frequency change per unit of time.

The intersyllable interval was the period of silence separating the syllable measured from the syllable that followed it. This measurement was taken only between like syllables.

As measures of repertoire size, we determined the number of different syllables used by each male in all songs, as well as the number of song types used by each male (after Lemon 1965). Both the number of different syllables and the number of song types sung by each male correlated significantly with the number of songs recorded ($r = 0.69$ and 0.73 , respectively; $P < 0.001$). Thus, to correct for differences in numbers of songs recorded, we calculated regression equations for each male to obtain a "predicted" number of syllables or song types for a given number of songs recorded. A log transformation of the number of songs corrected for a slightly parabolic relationship between songs recorded and both variables. We used, as new variables, the residuals for each observation (the difference between the observed number of syllables, or song types, and the predicted) that were calculated by the regression program [residual for the number of syllables (RESB): $r^2 = 0.56$, $n = 30$, $F_{1,28} = 36.2$, $P < 0.001$; residual for the number of syllable types (REST): $r^2 = 0.72$, $n = 30$, $F_{1,28} = 70.9$, $P < 0.001$; Table 1].

To evaluate song complexity, we calculated an index of syllable versatility within songs for each cardinal. Modifying a technique developed by Kroodsma and Verner (1978), total syllable-type versatility was defined as a ratio between the sources of within-

song variation and the total number of syllables in a song. The formula for syllable-type versatility is written as:

$$\text{syllable-type versatility} = (a \times b)/c,$$

where a = number of different syllables/song, b = number of syllable transitions/song, and c = total number of syllables/song.

In addition to syllable-type versatility, we calculated total versatility of song types per male (SGVS) and transitions between song types as described by Kroodsma and Verner (1978) (Table 1). Song types were listed in sequence, and 10-song sequences were used to calculate total song versatility. If fewer than 11 songs were sung in a bout, total song versatility was not calculated.

Territory mapping.—We delineated the territories of Northern Cardinals by intensive spot-mapping, noting the outmost limits where each male sang (International Bird Census Comm. 1970), by observing movements of males in great detail, and sometimes by flushing males. Male and female cardinals were captured at 11 different mist-net stations (each station had a 2.1×12.8 -m net with 3.8-cm mesh) set up throughout the study area, color marked, and released. Poor visibility and impenetrability of vegetation precluded extensive use of Wiens's (1969) flushing technique. A 40-m grid with numbered stakes and flagged poles positioned at all intersections of grid lines provided reference points for mapping territories on the entire 15-ha study area. About 230–250 h were spent from the end of March to 15 June each year (1979–1981) to determine territory boundaries. Territories were drawn on maps of the study area, cut out, and their areas measured with a LiCor conveyor belt (LI-3000) area meter.

Sampling territory vegetation.—The geometric center of each cardinal territory was located in the field by using grid maps. Three plots, 8 m in radius (0.02 ha), were centered 20 m from each territory center at compass bearings of 90° , 210° , and 330° . The height and species of trees greater than 5 cm in diameter at breast height (DBH), basal area, maximum height of vegetation, percentage of canopy closure, and foliage density were measured within these plots (Table 2).

The directions for foliage density measurements, either north and east or south and west, were determined randomly for each plot. Foliage density was estimated for ground level and for 1-, 2-, and 3-m height intervals with a 0.5-m-square (0.25 m²) gridded board (MacArthur and MacArthur 1961). Mid-story and canopy foliage density (higher than 7 m) and percentage of canopy closure above 20 m were estimated with a reflex camera (MacArthur and Horn 1969) positioned at the center of each 0.02-ha plot. Foliage height diversity (MacArthur and MacArthur 1961) and estimates of vertical and horizontal patchiness were calculated for each territory (Table 2). Vertical patchiness was calculated by subtracting foliage

TABLE 2. Habitat characteristics measured within 27 cardinal territories in eastern Texas.

Variable code	Description	Mean	SD
TF0-3	Total foliage density, ground to 3 m (m ² /m ³)	0.60	0.25
FDG	Foliage density, ground level (m ² /m ³)	0.27	0.17
FD1	Foliage density, 1 m (m ² /m ³)	0.13	0.05
FD2	Foliage density, 2 m (m ² /m ³)	0.12	0.06
FD3	Foliage density, 3 m (m ² /m ³)	0.08	0.04
FD7	Foliage density, 7-13 m (m ² /m ³)	0.04	0.06
FD13	Foliage density, 13-20 m (m ² /m ³)	0.04	0.06
FD20	Foliage density, >20 m (m ² /m ³)	0.20	0.37
%CC	Canopy closure (%)	26.85	25.36
VHGT	Vegetation height (m)	13.41	6.70
#TRSP	No. of tree species	3.12	1.97
#TRES	No. of tree stems >6 cm	7.47	3.95
TSPD	Tree species diversity (<i>H'</i>)	0.79	0.55
BA	Basal area (m ² /ha)	8.21	5.18
#SHSP	No. of shrub species	8.37	4.92
#SHRB	No. of shrub stems	29.96	13.93
SSPD	Shrub species diversity (<i>H'</i>)	4.24	2.16
%GC	Ground cover (%)	42.91	26.73
TSIZ	Territory size (ha)	0.64	0.14
ARBM	Arthropod biomass (g)	3.78	1.52
HPTCH	Horizontal patchiness at 2 m (1 - <i>J'</i>)	0.09	0.13
VPTCH	Vertical patchiness (1 - <i>J'</i>)	0.11	0.07
FHD	Foliage height diversity (<i>H'</i>)	1.24	0.09

height equitability (*J'*) from 1.0. Horizontal patchiness of shrub-level vegetation at 1, 2, and 3 m was estimated for each territory by calculating the equitability of the sums of foliage densities at each horizontal foliage sampling point and subtracting it from 1.0.

A smaller subplot (3 per territory), 1.8 m in radius (0.001 ha), was established within each 0.02-ha plot. It was randomly located 3 m from the center of the plot. The species and number of stems of all woody vegetation less than 6 cm DBH, percentage of ground cover, and average height of shrubby vegetation (vegetation <3 m high) were measured in this subplot (Table 1). Shrub species diversity (*H'*) and equitability (*J'*) were calculated. Percentage of ground cover was determined by looking straight down through a tube, 11 cm long and 4 cm in diameter, at the center of the subplot from 1.3 m above the ground and estimating the proportion of herbaceous cover to bare ground.

Nest observations.—While territories were being mapped and songs recorded, we searched the study area for cardinal nests. Only what we believed to be first nesting attempts were evaluated. After a nest was located, we visited it every day or two to check how many eggs or young were present. We used a mirror on the end of a pole to examine nests above eye level. Young cardinals were considered to have fledged successfully if they were seen in the nest until at least 9 days old and subsequently were not found in an undisturbed nest (Table 3). Typically,

fledglings could be heard begging for food in shrubs near their nest site. Our presence may have influenced nest success (Bart and Robson 1982). The disturbance factor should have been fairly equal in all territories because all nests were visited at an equal rate, and territories in general were traversed at equivalent frequencies while mapping bird positions and recording male song. Unsuccessful nests were classified according to the most likely cause for failure: fire ant (*Solenopsis invicta*) predation or Brown-headed Cowbird (*Molothrus ater*) parasitism; undisturbed empty nest—snake or bird predator; and disturbed empty nest—mammalian predator (Best 1978).

Sampling nest-site vegetation.—An 8-m-radius plot (0.02 ha) was centered on each nest site to sample vegetation (Table 3). Foliage densities, basal area, and vegetation height were measured in the same manner as for the territory plots. At each nest, the height of the nest tree and height of the nest above ground were measured with a metric tape when possible, and otherwise with an Abney level. Estimates of nest concealment were obtained with the aid of a 0.5-m-square density board similar to the board used by MacArthur and MacArthur (1961). The board was positioned vertically 0.5 m from the nest on both a north-south and east-west bearing to estimate concealment from horizontal directions. The observer, facing the board 0.5 m from the nest on the opposite side of the nest from the board (1 m from the board), looked through the vegetation and estimated the percentage of the board that was obscured by foliage. This pro-

TABLE 3. Characteristics measured at 30 cardinal nest sites in eastern Texas.

Variable code	Description	Mean	SD
NFDG	Foliage density, ground level at nest site (m ² /m ³)	0.28	0.18
NFD1	Foliage density, 1 m at nest site (m ² /m ³)	0.23	0.16
NFD2	Foliage density, 2 m at nest site (m ² /m ³)	0.32	0.56
NFD3	Foliage density, 3 m at nest site (m ² /m ³)	0.15	0.17
NFD7	Foliage density, 7-13 m at nest site (m ² /m ³)	0.02	0.07
NFD13	Foliage density, 13-20 m at nest site (m ² /m ³)	0.02	0.04
NFD20	Foliage density, >20 m at nest site (m ² /m ³)	0.29	1.40
NVHGT	Vegetation height at nest site (m)	11.98	8.10
NBA	Basal area at nest site (m ² /ha)	7.43	5.68
NHGT	Nest height (m)	1.58	0.73
HTNT	Height of nest plant (m)	2.88	0.99
FDHZ	Horizontal foliage concealment of nest (%)	45.09	26.51
FDVT	Vertical foliage concealment of nest (%)	64.57	26.37
FLDG	No. of young fledged/nest	0.70	0.97
YONG	Maximum number of young in nest	1.04	1.15
EGGS	Maximum number of eggs in nest	2.04	0.82

cedure was repeated with the board 0.5 m above the nest and the observer 0.5 m below the nest to estimate vertical concealment. We did not measure concealment above the nest separately from concealment below the nest.

Arthropod sampling.—A crude estimate of food availability was obtained by sampling each territory with 38-cm-diameter insect sweep nets. Although not a direct sample of cardinal food, we assumed that our measure of arthropod biomass would give a relative index of the overall food availability. Five 200-sweep samples (1,000 sweeps/territory) were taken from random places on 5 different days immediately following nesting in each territory. These samples were oven dried for 48 h and weighed on an analytical balance.

Data analyses.—Of 43 territories located and studied, only 21 had measurements for all variables (≥ 89 songs recorded and all nest data). Correlation analyses were used to examine degrees of association between variables. We realize that there are potential problems associated with interpretations of multiple bivariate correlations if conclusions are focused on individual correlations. We have evaluated patterns of numerous significant correlations in this paper to gain insight into ecological relationships. Although many significant correlations were detected, we present only those relevant to relationships among territory size, habitat, song, and nesting success of Northern Cardinals. Sample sizes for evaluating degrees of relationship varied: nesting success vs. song variables, $n = 21$; nesting success vs. territory size, arthropod biomass, and vegetation variables, $n = 23$; and song vs. territory size, arthropod biomass, and vegetation variables, $n = 30$. Discriminant function analysis (Hull and Nie 1981) comparing territories that fledged young vs. those not fledged young ($n =$

21), was used to evaluate variables that might be important to nesting success. Rao's V was used as the stepwise selection method, with an F value of 3.2 set for entry of variables into the analysis. Because of unequal group sample sizes, we checked the influence of heteroscedasticity by making a log transformation on all variables and recalculating the discriminant function (DFA). The results of the DFA using log-transformed variables were consistent with the DFA using raw data, indicating the acceptability of the initial DFA (Pimentel 1979).

RESULTS

Cardinal territory size was related to vegetation structure. Territory size was positively correlated with vegetation height and negatively correlated with total foliage density from the ground up to 3 m, foliage density at ground level, and number of shrubs (Table 4). Thus, territories were larger in areas having mature trees and smaller where only shrubby vegetation was present. Previous studies have indicated that cardinals have a strong affinity for understory foliage (Dow 1970, Conner et al. 1983) and often nest in shrubs (Stauffer and Best 1980). Because understory foliage was negatively correlated with overstory foliage (percentage of canopy closure was negatively correlated, $P < 0.001$, with understory foliage variables: FDG, $r = -0.69$; FD1, $r = -0.58$; FD2, $r = -0.58$; and TF0-3, $r = -0.76$), the increase in cardinal territory size in areas where mature trees were present was not surprising. Cardinals may require a threshold amount of under-

TABLE 4. Correlations of habitat, song, territory size and quality, and nesting success of Northern Cardinals (see Tables 1–3 for variable codes). Sample size varies for the entries in this table; see Methods. Correlations with $P > 0.10$ and variables without any significant correlations are omitted from the table.^a

	TSIZ	ARBM	SBVS	ASYB	SGVS	RESB	YONC ^b	FLDG ^b
TSIZ					0.25 ^c			
ARBM			-0.34*	-0.40*			0.45*	0.40*
SBVS		-0.34*			0.32*		-0.36 ^c	
SGVS	0.25 ^c		0.32*					
SLGT		-0.45**		0.83***				
%GC		0.72***		-0.42*				
FDG	-0.43**	0.57***					0.43*	0.40*
FD1		0.64***		-0.34*			0.37*	0.37*
FD2						0.41*		0.51**
FD3	-0.46**		-0.30 ^c		-0.36*			
TF0-3	-0.45**	0.51**			-0.29 ^c	0.33*	0.38*	0.45*
FD20								
SSPD		0.54***	-0.53***			0.32*		
#SHRB	-0.37*							
HPTCH								0.41*
VHGT	0.40**	-0.33*			0.33*		-0.30 ^c	-0.28 ^c
#TRES		-0.44**					-0.38*	-0.46*
BA		-0.53***					-0.39*	-0.44*

* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

^b Spearman rank correlations.

^c $P < 0.10$.

story foliage in their territories. If shrub foliage is sparse, territory size may be increased to compensate.

Arthropod biomass was positively correlated with foliage density at ground level and at 1 m, total foliage density at 0–3 m, percentage of ground cover, and shrub species diversity (Table 4). Arthropod biomass was negatively correlated with number of trees, basal area, and vegetation height.

Total syllable versatility (SBVS), our measure of within-song complexity, was negatively correlated with arthropod biomass, foliage density at 3 m, and shrub species diversity (Table 4). The average number of syllables used in each song and song length also correlated negatively with arthropod biomass. These results suggest that cardinals having the shortest and least versatile songs were on the best-quality territories. Total song versatility correlated positively with total syllable versatility but was not correlated with arthropod biomass. No other song variable was significantly correlated with arthropod biomass ($P > 0.05$).

Of our measures of repertoire size, only the residual of the number of syllables sung by males (RESB) was positively correlated with foliage density at 2 m, total foliage density from the ground to 3 m, and shrub species diversity

(Table 4). This suggests an association between large syllable repertoires and vegetation characteristic of good-quality territories. Although understory foliage variables and shrub species diversity were correlated with arthropod biomass, the residual of the number of syllables was not. The residual of the number of syllables also was not significantly correlated with any measure of nesting success.

Nesting success in the long run should be the best index to what *might* be quality habitat. Although our study was only 3 years in length, some relationships were observed. Fledging success and number of young in nests were positively correlated with arthropod biomass (Table 4). The number of eggs in nests was not correlated with arthropod biomass or any other variable measured. We had originally expected clutch size to be related to food availability. Fledging success and the number of young in nests were also positively correlated with foliage density at the ground, at 1 m above the ground, and with total foliage density at 0–3 m. In addition, fledging success was positively correlated with foliage density at 2 m and horizontal patchiness at 2 m above the ground. Both fledging success and the number of young in nests were negatively correlated with the number of trees and tree basal area (Table 4).

Collectively, these results suggest that the better-quality territories were areas with fewer trees and more understory foliage. Originally, we had expected some aspect of nesting success to be positively correlated with territory size, but none was.

No significant correlation between fledging success and nest height existed ($r_s = 0.01$, $P > 0.05$). However, territories with successful nests had higher foliage density and patchiness at 2 m throughout the territory than did territories with unsuccessful nests (ANOVA, $P < 0.05$). This suggests that abundance and distribution of foliage at 2 m above the ground throughout the territory may be important for cardinals. This is reinforced by the fact that cardinal nests in the study averaged 1.6 m above the ground.

Nesting success variables were not significantly correlated with cardinal song characteristics ($P > 0.05$). However, total syllable versatility had a nearly significant negative correlation with number of young in nests ($r_s = -0.36$, $P < 0.053$). Studies conducted over a longer period of time with a larger sample are probably needed to demonstrate strong relationships between song characteristics and nesting success.

Cowbird parasitism and predation affected nesting success. Causes of nesting failures in our study area over 3 years were: 7 to Brown-headed Cowbird parasitism, 5 to small mammals and snakes, 1 to a large mammal, and 1 to fire ants. We observed partial clutch losses on 9 occasions, which may have caused an absence of correlation between the number of eggs and the number fledged ($r_s = 0.08$, $P > 0.05$). The number of young and the number fledged were significantly correlated (Spearman rank correlation, $r_s = 0.70$, $P < 0.001$). Also, nests found in early stages of the nesting cycle (nest building and egg-laying) may have had a higher probability of parasitism than nests found during the nestling phase (Mayfield 1961). Although we expected nest concealment to have an effect on nest parasitism and predation, no significant correlations existed between fledging success and foliage density in the nest vicinity (NFD1 through NFD3, Table 3) or nest concealment (FDHZ and FDVT).

A stepwise 2-group DFA using song and territory variables (Tables 1, 2) successfully discriminated between territories having successful nests (nests fledging at least one young) and

TABLE 5. Correlations of original territory and song variables with the discriminant function (canonical variate) resulting from a 2-group DFA used to discriminate between territories successfully fledging young ($n = 7$) and territories where nests failed ($n = 14$). (See Tables 1-3 for variable codes and units.)

Variable	Pearson correlation*
FD2	0.75***
HPTCH	0.64***
SLGT	-0.60**
VPTCH	0.57**
TF0-3	0.54**
FHD	-0.53**
FD1	0.51**
ARBM	0.47**
ASYB	-0.46*
#TRES	-0.43*
VHGT	-0.41*

* * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$.

territories having unsuccessful nests ($P < 0.006$, 90.5% of cases correctly classified, eigenvalue of the discriminant function = 1.048). Three variables entered the stepwise DFA: foliage density at 2 m, song length, and versatility of syllables per song. Examination of the correlations of the original territory and song variables with the discriminant axis (canonical variate) indicated that successful nests were positively associated with increasing values of foliage density at 2 m, horizontal patchiness at 2 m, vertical patchiness, total foliage density from the ground to 3 m, foliage density at 1 m (i.e. dense, patchy understory foliage), and arthropod biomass (Table 5). Successful nests were negatively associated with increasing song length, foliage height diversity, number of syllables per song, number of tree stems, and vegetation height. Thus, unsuccessful nests were associated with increasing vegetation height, density of trees, and foliage height diversity, and male territorial cardinals that sang long songs with higher within-song versatility. Results of the DFA agree closely with our interpretation of the correlation patterns among the univariate variables (Table 4).

DISCUSSION

Our results suggest some interesting relationships. Cardinals with less versatile or complex songs may hold better-quality territories (territories with more understory foliage and

TABLE 6. Song characteristics of a male cardinal that held the same territory for three successive breeding seasons (see Table 1 for variable codes and units).

Year	NSGS	SBVS	ASYB	DSYB	TRAN	SLGT	SBRP
1979	316	0.094	7.1	1.4	0.36	1.96	18
1980	398	0.140	7.5	1.5	0.50	2.41	17
1981	187	0.177	11.6	1.8	0.78	2.49	18

greater arthropod biomass) and fledge more young than cardinals with more complex songs. This suggests that natural selection would favor males with the least song complexity, a concept that at first appears counterintuitive.

Several alternative explanations may clarify this apparent contradiction. Fledging success may be confounded by factors other than overall territory quality. Predation and nest parasitism can both greatly affect nesting success and yet not be related to territory quality from a "food" perspective. Our visits to nests may have increased the probability of cowbird parasitism and predation. Although nest concealment should be related to cowbird parasitism and predation, our measurements of concealment may have been insufficient to document this relationship. Wray and Whitmore (1979) made more extensive measurements of nest concealment than we did and detected a significant relationship between foliage proximal to the nest and nesting success.

Our measures of song complexity and repertoire size may also be confounded. Howard (1974) speculated that both repertoire size and reproductive success might be correlated with age. A study of the Great Tit (*Parus major*) demonstrated that males with intermediate-size repertoires have the highest lifetime reproductive success (McGregor et al. 1981). Older male White-crowned Sparrows (*Zonotrichia leucophrys*) hold larger territories and are more often successful in breeding than young males (Ralph and Pearson 1971). Male Field Sparrows (*Spizella pusilla*) with larger territories mate more frequently than males with smaller territories (Best 1977).

Young male cardinals may use longer, highly complex songs when first establishing a territory. In subsequent breeding seasons, age or prior ownership of a particular territory may permit the male to put "less effort" into song (complexity) and allow more effort for nest defense and care of young. This hypothesis meshes with our results of song complexity being

negatively related to fledging success. However, this hypothesis also suggests that song complexity should decrease over successive years. Such was not the case with one male cardinal that nested in the same territory for 3 consecutive years. Total syllable versatility, number of syllables per song, number of different syllables used per song, and song length increased steadily for this individual during the study (Table 6). Syllable repertoire (SBRP) for this male remained relatively constant, and no trend or pattern was observed with other song variables. Similarly, repertoires of Great Tits also do not increase yearly (Krebs et al. 1978). The change we observed in song complexity over time for one male cardinal is obviously insufficient to establish any trends. Studies on additional males are needed to provide sufficient data for a more accurate determination.

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