Journal of Wildlife Diseases, 27(2), 1991, pp. 185-205
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ECOLOGY OF HELMINTH PARASITISM IN BOBWHITES FROM NORTHERN FLORIDA

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ABSTRACT: Examination of 700 northern bobwhites (*Colinus virginianus*), 50 each February from 1971 through 1984, from Tall Timbers Research Station, Leon County, Florida, disclosed 15 species of helminth parasites. Nine species (*Raillietina cesticillus, R. colinia, Aproctella stoddardi, Cheilospirura spinosa, Cyrnea colini, Dispharynx nasuta, Heterakis isolonche, Tetrameres pattersoni*, and *Trichostrongylus tenuis*) generally were found on an annual basis and were considered characteristic components of the helminth fauna. Infrequently found species were *Brachylecithum nanum, Rhabdometra odiosa, Capillaria* sp., *Gongylonema ingluvicola, H. gallinarum*, and *Oxyspirura matogrosensis*. Intensities of *C. colini* and *H. isolonche* differed among host sex and age classes, and prevalences and/or intensities of *A. stoddardi, C. spinosa, T. pattersoni*, and *T. tenuis* differed between host age classes. Prevalences and/or abundances of seven species (*R. cesticillus, R. colinia, C. spinosa, C. colini, H. isolonche, T. pattersoni*, and *T. tenuis*) varied with bobwhite density, apparently because bobwhites were either the primary or only definitive host on the area. Two species (*A. stoddardi* and *D. nasuta*) did not vary with bobwhite density, apparently due to the buffering effect of a broad range of definitive hosts on the area. Prevalences and/or intensities of *R. colinia, C. spinosa*, and *T. tenuis* differed with agricultural fields status (cultivated versus fallow) suggesting that land use and its attendant habitat changes influenced transmission of these species. The occurrence of *C. spinosa* and *T. pattersoni* in individual bobwhites was not independent and was attributed to utilization of the same species of grasshoppers as intermediate hosts. Localized tissue damage and inflammation were associated with *A. stoddardi, D. nasuta, C. spinosa, C. colini* and *T. pattersoni*. Decreases in body weight in juvenile bobwhites were associated with increasing intensities of *H. isolonche* and *T. tenuis*. The observed relationships to bobwhite density and other variables are discussed with regard to known aspects of life histories of the nine most common species.

Key words: Northern bobwhite, quail, *Colinus virginianus*, helminths, parasitism, host density, ecology.

INTRODUCTION

The numerous reports (see literature reviews by Kellogg and Calpin, 1971; Kellogg and Doster, 1972) on parasitism in northern bobwhites (*Colinus virginianus*) provide little information on the relationship between parasitism and host population fluctuations. A general association of high levels of parasitism in wild bobwhite populations subjectively categorized as dense or crowded has been reported on several occasions (Cram et al., 1931; Parmalee, 1952; Kellogg and Prestwood, 1968). Forrester et al. (1984) hypothesized that changes in bobwhite density could have been responsible for observed differences in helminth infections among years in Florida, and Moore et al. (1988) suggested that bobwhite covey size might influence parasitism by some species of helminths. None of these studies, however, examined the relationship of host density to parasitism over numerous consecutive years in populations where bobwhite density was objectively quantified.

The present study derives from a series of continuing, long-term multifaceted investigations on bobwhite diseases and

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management (for reviews see Davidson et al., 1982; Dimmick et al., 1982; Doster et al., 1982; Pollock et al., 1989; Smith et al., 1982). This portion of the investigation was designed to further elucidate certain aspects of the ecology of helminth parasitism among bobwhites. Specific objectives were to: (1) determine the composition of the helminth community and monitor changes in its composition over numerous consecutive years; (2) obtain information on the distribution of helminths among different sex and age classes of bobwhites; (3) investigate associations between certain species of helminths; (4) examine the relationship between agricultural activities and parasitism among bobwhites; (5) further delineate the role of helminths as pathogens in bobwhites; and (6) examine the relationship between bobwhite density and helminth parasitism. Major emphasis is placed on the relationship of helminth parasitism to bobwhite density.

MATERIALS AND METHODS

The study was conducted at Tall Timbers Research Station (TTRS), a 1,120-hectare area (30°39′N; 84°13′W) located in a limestone region of broken terrain in the northern part of Leon County, Florida (USA). Two study sites (202 and 210 ha) were utilized and have been described elsewhere (Kellogg et al., 1972; Smith, 1980). Small fields on Study Site 1 were planted in corn during the summers of 1968 to 1971 and 1975 to 1983, while small fields on Study Site 2 were planted in corn in 1968 and 1972 to 1982. Fields were tilled in February or March and again in April or May during corn planting operations. Corn was harvested with a mechanical picker in October. During the remaining years, fields were left fallow and did not receive any treatments while they were fallow, except that approximately one-half of each field was harrowed on Study Site 2 in spring of 1983 as part of studies by other researchers. Agricultural chemicals were not used during farming activities. Controlled burning was conducted annually over the majority of both study sites during late February or early March upon completion of bobwhite parasite studies. Prior to 1976, fields were protected from controlled fires. After 1976, fields were not protected which resulted in light, patchy burns depending on amounts of fuel present.

Populations of bobwhites on both study sites were estimated annually each February from 1970 to 1984 using Lincoln index methodology (Kellogg et al., 1970, 1972; Dimmick et al., 1982; Smith et al., 1982; O'Brien et al., 1985). Bobwhite populations were not manipulated, other than by the influence of land management practices and approximately 25 to 30% annual removal during population estimates (Doster et al., 1982; Pollock et al., 1989). A single exception was that following parasite studies in February 1975, bobwhite density was intentionally reduced to 0.25 per hectare on Study Site 2. Detailed descriptions of the history, study sites, land management practices, and bobwhite population characteristics at TTRS have been presented (Kellogg and Doster, 1971; Kellogg et al., 1970, 1972; Komarek, 1977; Dimmick et al., 1982; Doster et al., 1982; Smith, 1980; Smith et al., 1982; Pollock et al., 1989).

Twenty-five bobwhites collected from each study site during population estimates were examined at necropsy. A stratified random sampling system was employed to ensure representation of bobwhite age and sex classes in general proportion to the population at large (Pollock et al., 1989) and to achieve spatial distribution over the study sites. Not more than three bobwhites per covey were used for parasite studies. Techniques of necropsy and helminth recovery and enumeration methods have been described (Kellogg and Prestwood, 1968; Barrows and Hayes, 1977; Davidson et al., 1980). Voucher specimens were filed with the U.S. National Parasite Collection, Beltsville, Maryland under accession numbers 74319 and 75848 to 75854. Terminology referring to various parameters of parasitism is that of Margolis et al. (1982).

Statistical analyses were conducted in two stages as the study progressed. The first analyses were conducted on 500 bobwhites collected over 10 yr (1971 to 1980). These analyses examined (1) the relationship of each common species of helminth to the variables of host sex and age, and (2) interspecific relationships between selected common species. Specific analyses were (1) a split plot design analysis of variance (ANOVA) (with study site as the main plot effect, year as the random element, and sex and age as the split-plot effects) utilizing the General Linear Models (GLM) procedures of SAS Institute, Inc. (1985) to examine the prevalence and mean intensity of each common species within different host sex and age categories; and (2) a Chi square test to compare the co-occurrence (association) of selected species in individual bobwhites.

The remaining statistical analyses were conducted using data from all 700 bobwhites (1971 to 1984). These analyses examined (1) the relationships of prevalence and abundance of each common species to bobwhite population den-

sity, (2) the relationships of prevalence and abundance of common species to agricultural land use (fields cultivated versus fallow), and (3) the relationship of the intensity of infection with selected species to host body weight. Specific analyses were (1) covariance analysis on annual prevalence and abundance for each common species using current (within) year and the preceding year's (lag effect) bobwhite densities as covariates for the study site effect ($n = 28$, each analysis), (2) a randomized complete block design analysis of variance with current year bobwhite population density as a covariate for evaluation of agricultural land use ($n = 10$, each analysis), and (3) pairwise t-tests to detect differences between the mean weights of bobwhites (segregated by age class) harboring various intensities of selected species. In analyses of host density relationships, the combination of current and preceding year's host density was adopted when correlated errors were detected (indicating that parasitism was not totally independent of the previous year's host density).

To stabilize variances and to approximate normality, prevalence data were transformed using the arcsin root proportion transformation and count data were transformed using a logarithmic transformation [$\log_{10}$(count + 1)]. ANOVAs and regression models above were fit using the GLM procedure of SAS (SAS Institute, Inc., 1985). All references to significant differences refer to $P \leq 0.05$ for the above analyses.

Data on bobwhite population densities at TTRS in February, 1970 were obtained for comparative purposes (Kellogg et al., 1970) and included as an informational aid in figures. Figures were prepared utilizing software (Harvard Graphics, Version 2.1, Software Publishing Corp., Mountain View, California 94040, USA) which fits a curve to plotted data points. This smoothing procedure is useful with time sequence and trend data; however, the curves do not actually connect the values and actual data points should be examined along with the curves.

RESULTS AND DISCUSSION

Helminth community composition

From 1971 to 1984, 15 species of helminths were identified in 700 bobwhites (Table 1). Nine species generally were found on an annual basis and were considered characteristic components of the helminth fauna of bobwhites on TTRS. Seven of these species (*Raillietina cesticillus*, *R. colinia*, *Cheilospirura spinosa*, *Cyrnea colini*, *Heterakis isolonche*, *Tetrameres pattersoni*, and *Trichostrongylus tenuis*) have been reported to be common (≥30% prevalence) in bobwhites on TTRS during earlier studies (Davidson et al., 1980; Moore et al., 1986). The two remaining species, *Aproctella stoddardi* and *Dispharynx nasuta*, also have been reported from bobwhites at TTRS but at lower (≤20%) prevalences (Kellogg and Prestwood, 1968; Davidson et al., 1980; Moore et al., 1986). Forrester et al. (1984) listed these same nine species as the most frequent in bobwhites from Leon County, Florida. These authors also considered most of these species to be characteristic components of the helminth fauna of bobwhites throughout Florida.

Based on their low prevalence in the present and other studies (Kellogg and Prestwood, 1968; Davidson et al., 1980; Moore et al., 1986), *Brachylecithum nanum*, *Rhabdometra odiosa*, *Capillaria* sp., *Gongylonema ingluvicola*, *H. gallinarum*, and *Oxyspirura matogrosensis* were considered unusual or accidental in bobwhites on TTRS. However, all of these species have been reported previously from bobwhites in the southeastern United States (Davidson et al., 1982). An additional five species (*Brachylaima* sp., *Hymenolepis* sp., *Mediorhynchus papillosis*, *Strongyloides avium*, and *Subulura* sp.) previously reported from bobwhites at TTRS during other seasons of the year (Byrd and Kellogg, 1971; Davidson et al., 1980; Moore et al., 1986) were not found during our studies in mid-winter.

Variation associated with host sex and age

Stratification of data by host sex (Table 2) revealed that abundances of *H. isolonche* and *C. colini* were higher ($P < 0.01$) in female than in male bobwhites (42% and 35% greater for *H. isolonche* and *C. colini*, respectively). Sex by age interactions ($P < 0.01$) were noted with the abundance of both species. In adult bobwhites, numbers of these parasites in females exceeded those in males by a substantial margin (143% and 94% higher for *H. isolonche* and *C. colini*, respectively).

TABLE 1. Prevalence, abundance, mean intensity and maximum number, and number of years each species of helminth was detected in 700 bobwhites from Tall Timbers Research Station, 1971 to 1984.

Species	Prevalence	Abundance	Mean intensity	Maximum number	Number years detected
Brachylecithum nanum	0.1	<0.01	3.00	3	1
Raillietina cesticillus	14.8	1.38	9.38	107	10
Raillietina colinia	37.7	1.37	3.63	62	14
Rhabdometra odiosa	0.4	0.01	1.33	2	2
Aproctella stoddardi	4.4	0.08	1.84	7	12
Capillaria sp.	0.4	0.01	2.00	4	2
Cheilospirura spinosa	18.4	0.62	3.34	20	10
Cyrnea colini	90.3	4.10	4.52	28	14
Dispharynx nasuta	10.3	0.16	1.51	9	14
Gongylonema ingluvicola	1.3	0.03	2.00	7	6
Heterakis gallinarum	0.7	0.01	1.60	2	3
Heterakis isolonche	97.7	36.65	37.46	288	14
Oxyspirura matogrosensis	0.4	<0.01	1.00	1	2
Tetrameres pattersoni	27.1	1.34	4.94	38	14
Trichostrongylus tenuis	95.0	65.66	69.03	1,455	14

In contrast, the numbers in juvenile females were slightly less than those in juvenile males (83% and 94% as great for *H. isolonche* and *C. colini*, respectively). Thus, infections of *H. isolonche* and *C. colini* increased with age in females but decreased with age in males. This resulted in the adult females harboring more of these helminths than adult males. Factors responsible for these differences are unknown. Moore et al. (1987) presented evidence of limited influences of host sex or age on helminths of bobwhites, although the prevalence of *C. colini* larvae tended to be higher in female bobwhites during summer at TTRS. Analyses of data during their study were complicated by unavoidably small and unequal samples obtained over a period of several months. Unlike the present study, Forrester et al. (1984) found no relationship between host sex and prevalences or intensities of helminth infections in 381 bobwhites examined during winter over a 5-yr period from Charlotte County, Florida.

Stratification of data by host age (Table 2) disclosed that four species (*T. tenuis, C. spinosa, T. pattersoni*, and *A. stoddardi*) had higher ($P < 0.01$) prevalences and/or abundances in adult bobwhites. Because age by sex interactions were not significant for these species, the differences were related only to age. Previous studies also have disclosed higher, although generally not statistically significant, prevalences and/or intensities of *T. tenuis, C. spinosa*, and *T. patersoni* in adult bobwhites (Blakeney and Dimmick, 1971; Davidson et al., 1980; Moore et al., 1986, 1987). Moore et al. (1987) noted that in general host age, but not host sex, occasionally was an important factor influencing helminthiases of bobwhites. Host age-related differences for these species have been attributed to the shorter length of exposure of juvenile bobwhites and the time required for helminth development, which combine to produce a trend of increasing helminth infections as juvenile bobwhites become older (Davidson et al., 1980). Although the life cycle of *A. stoddardi* is unknown, opportunity for exposure to its hematophagus intermediate host probably is a factor in its lower prevalence and intensity in juveniles. Earlier studies of seasonal trends of helminth parasites of bobwhites at TTRS indicated that juveniles acquired most common species by July and that by January the helminth fauna of juveniles was essentially equivalent to that of adults (Davidson et al., 1980; Moore et al., 1986).

Unlike the present study, previous stud-

TABLE 2. Prevalence and mean intensity of common helminths by host sex and age in 500 bobwhites from Tall Timbers Research Station, 1971 to 1980.

Species (Sample size)	Parameter	Male (266)	Female (234)	P^a	Juvenile (367)	Adult (133)	P^b	Age•Sex[c]
Heterakis isolonche	Prevalence	97	99	NS[d]	94	99	NS	NS
	Intensity	34.0	42.0	<0.01	36.0	44.0	NS	<0.01
Trichostrongylus tenuis	Prevalence	95	96	NS	94	99	NS	NS
	Intensity	79.0	99.0	NS	75.0	124.0	<0.01	NS
Cyrnea colini	Prevalence	89	91	NS	92	90	NS	NS
	Intensity	4.1	4.7	<0.01	4.2	4.9	NS	<0.01
Cheilospirura spinosa	Prevalence	25	26	NS	21	40	<0.01	NS
	Intensity	3.4	3.3	NS	3.5	3.0	<0.01	NS
Tetrameres pattersoni	Prevalence	34	38	NS	26	58	<0.01	NS
	Intensity	4.5	5.2	NS	4.3	5.6	<0.01	NS
Raillietina cesticillus	Prevalence	17	18	NS	15	23	NS	NS
	Intensity	8.6	10.3	NS	9.9	8.3	NS	NS
Raillietina colinia	Prevalence	38	38	NS	40	31	NS	NS
	Intensity	3.9	4.3	NS	4.1	3.9	NS	NS
Dispharynx nasuta	Prevalence	10	13	NS	12	9	NS	NS
	Intensity	1.3	1.7	NS	1.3	2.9	NS	NS
Aproctella stoddardi	Prevalence	6	6	NS	2	15	<0.01	NS
	Intensity	2.4	1.1	NS	1.4	2.0	<0.01	NS

[a] P for difference in sex means.
[b] P for difference in age means.
[c] P for sex by age interaction.
[d] NS = not significant ($P > 0.05$).

ies have reported a higher prevalence of *D. nasuta* in juvenile bobwhites at TTRS (Davidson et al., 1980; Moore et al., 1986). During those studies, however, most juvenile birds were collected during summer or fall and were much younger than the 7- to 9-mo-old juveniles examined here. Hon et al. (1978) noted that wild turkey (*Meleagris gallopavo*) poults in central Florida had a peak prevalence (89%) of *D. nasuta* during August but by November prevalence had declined to virtually 0%. Acquired immunity, physiologic changes associated with age and dietary shifts have been suggested as factors that could produce the generally lower infections of *D. nasuta* in adult birds (Bendell, 1955; Hon et al., 1978; Rickard, 1985). Thus, the occurrence of equivalent prevalences of *D. nasuta* in the two age classes in this study is not unusual, considering the age of juveniles and the season when they were examined.

Evaluations of pathogenicity

Striking gross lesions were not encountered with infections of any species of helminth during this study, although local tissue damage and associated inflammation were noted occasionally with infections of *A. stoddardi*, *C. spinosa*, *C. colini*, *D. nasuta*, or *T. pattersoni*. Lesions were similar to those desribed elsewhere for these species (Kellogg and Prestwood, 1968; Barrows and Hayes, 1977; Davidson et al., 1977a, 1980, 1982; Rickard, 1985). Previous studies on bobwhites from TTRS (Davidson et al., 1980; Kellogg and Prestwood, 1968) and other areas of the southeastern United States (Palermo and Doster, 1970; Davidson et al., 1982; Forrester et al., 1984) similarly have revealed minimal gross lesions. In a review of diseases and parasitism among bobwhites, Davidson et al. (1982) concluded that helminths usually are not important as direct causes of mortality in adult wild bobwhites.

TABLE 3. Mean weights (g) of adult and juvenile bobwhites stratified by the intensity of infection with *Heterakis isolonche* or *Trichostrongylus tenuis*.[a]

Heterakis isolonche			*Trichostrongylus tenuis*		
Intensity	Adult	Juvenile	Intensity	Adult	Juvenile
≤20	169.9[a,b] (64)	165.8[a] (241)	≤50	169.5[a] (122)	165.1[a] (403)
21–40	166.8[a] (51)	165.3[a] (118)	51–100	166.8[a] (28)	167.7[a] (44)
41–80	168.6[a] (43)	163.3[a,b] (102)	101–200	163.7[b] (18)	167.2[a] (23)
81–160	166.8[a] (29)	162.8[b] (36)	201–400	163.9[b] (11)	159.5[b] (20)
≥161	173.3[b] (3)	160.1[b] (9)	≥401	171.2[a,c] (11)	153.5[c] (16)

[a] Numbers in parentheses indicate the number of bobwhites from which the mean weight was calculated. Column values with different alphabetic superscripts are different ($P \leq 0.05$).

Since subclinical parasitism often is associated with underweight or unthrifty hosts and because a previous study on bobwhites from TTRS suggested parasitism might be associated with lowered body weights and fat reserves (Dabney and Dimmick, 1977), body weight was utilized as a parameter for judging possible subclinical effects of parasitism. Adult and juvenile bobwhites were evaluated independently since our records indicated that mean weights for adults were nearly always 3–8 g higher than juveniles during any given year (W. R. Davidson, unpubl. data). Comparisons of mean weights of birds harboring *R. colinia*, *C. colini*, *C. spinosa*, *D. nasuta*, or *T. pattersoni* did not reveal any differences ($P > 0.05$) between bobwhites with lower and higher intensity infections. In contrast, body weights were lower among bobwhites with higher intensities of either *H. isolonche* or *T. tenuis*, especially among juveniles (Table 3). Data in Table 3 suggests that intensities of above approximately 40 *H. isolonche* or 200 *T. tenuis* may be related to decreased body weight among juvenile bobwhites. It is emphasized that this study was not designed to prove causal relationships between these parameters. In addition, sample sizes of more heavily infected bobwhites were not sufficient to allow partitioning for evaluation of the influence of other variables, such as bobwhite density, cultivation of fields, or annual food supply, which also may be determinants of either parasite intensity or body weight. However, when combined with prior reports of the detrimental effects of these species (Ruff, 1984; Wilson, 1982), our results suggest that *H. isolonche* and *T. tenuis* may produce subtle, subclinical disease when present in sufficient numbers.

Variations associated with host density and land use

A major consideration during this study was evaluation of the relationship of host density to helminth parasitism that was afforded by accurate bobwhite population estimates (Dimmick et al., 1982; O'Brien et al., 1985). During the 14-yr period of study, bobwhite densities on the study sites varied from a relatively low value of 0.75/ha to an extremely high value of 7.75/ha (Kellogg et al., 1970, 1972; Smith, 1980; Smith et al., 1982; Dimmick et al., 1982; O'Brien et al., 1985). Thus, bobwhite densities encompassed most values that would be expected under usual circumstances. Furthermore, bobwhites on TTRS are sedentary, with 86% found <400 m and 98% <800 m from where they had been captured 12 to 48 mo earlier (Smith, 1980; Smith et al., 1982). This sedentary behav-

ior reduced the potential for helminth introduction from adjacent areas.

Comparison of data on helminth parasitism with bobwhite density revealed that prevalences and/or abundances of seven of the nine most common species were related to bobwhite density (Table 3). These nine species are discussed individually below. The nature of the relationship of host density to parasitism varied among species and in many instances appeared to be attributable to differences in helminth life cycle patterns. For clarity, a brief synopsis of the life cycle of each species, including specific information from previous studies at TTRS, precedes data from the present study.

Heterakis isolonche (=*H. bonasae*)

The cecal worm, *H. isolonche*, has a monoxenous life cycle, although it may possibly utilize earthworms as paratenic hosts as does *H. gallinarum* (Reid, 1967; Davidson et al., 1977a, 1980). Unembryonated eggs shed in feces develop to contain infective larvae in 14 days at 27C (Davidson et al., 1978). Prepatent periods in experimentally infected bobwhites were 27 to 38 days (Davidson et al., 1978), and parasite longevity was as much as 210 days (Kellogg and Reid, 1970). In studies at TTRS, young bobwhites acquired *H. isolonche* by July, and prevalence was 90 to 100% by September (Davidson et al., 1980; Moore et al., 1986). Intensity increased with age in juveniles and approached the intensity in adults by January (Davidson et al., 1980). Although transmission of *H. isolonche* occurred to some extent throughout the year at TTRS, peak acquisition appeared to be from March to July, and *H. isolonche* was the predominant cecal nematode in bobwhites from August to November (Davidson et al., 1980). Bobwhites are the only known host for *H. isolonche* at TTRS.

Prevalence of *H. isolonche* was not related to bobwhite density on either study site (Table 4). Stable high prevalences (>88%) were maintained on both study sites (Fig. 1) even though there was a 10-fold difference between the lowest and highest bobwhite densities. Other studies at TTRS (Kellogg and Prestwood, 1968; Davidson et al., 1980; Moore et al., 1986) also have revealed consistently high prevalences of *H. isolonche* throughout the year. Forrester et al. (1984) likewise reported a high prevalence (90%) of *H. isolonche* in bobwhites from another location in Leon County. The maintenance of this high prevalence despite major fluctuations in bobwhite density in our study indicates a highly efficient life cycle. This efficiency may be largely attributable to the monoxenous life cycle and certain behavioral traits of bobwhites. Opportunity for completion of a monoxenous life cycle would appear to be optimal in a relatively sedentary, seasonally gregarious, ground-feeding species such as bobwhites. In addition, infective larvae of *Heterakis* remain within the protective covering of the egg while in the environment and thereby persist in a viable state for months (Reid, 1967). The extended survival of eggs containing larvae, along with the possible alternative of earthworm paratenic hosts, probably increases chances that bobwhites will become infected.

In contrast to prevalence, abundance of *H. isolonche* varied with bobwhite density on both study sites (Table 4; Fig. 1). Abundance most closely fit a model that incorporated only bobwhite density for the preceding February (Table 4); thus, *H. isolonche* tended to exhibit a lag effect of one year. If a causal relationship is assumed between bobwhite density and abundance of *H. isolonche*, then R^2 values suggest that approximately 39% of the variability would be attributable to bobwhite density. We believe this relationship is causal because bobwhites are the only reported definitive hosts for *H. isolonche* at TTRS. Thus, the occurrence of the parasite on the area was totally dependent upon bobwhites. Further, an earlier study (Davidson et al., 1980) showed that the major period of acquisition of *H. isolonche*

TABLE 4. Model probability values, estimated regression functions, and R^2 values for the prevalence and abundance of nine common species of helminths in bobwhites.

Species	Parameter (site)[a]	$P > F$	Model[b]	R^2 value
Heterakis isolonche	Prevalence (1, 2)	NS	None	NA
	Abundance (1, 2)	<0.005	$Y_t = 1.32 + 0.78X_{t-1}$	0.3949
Trichostrongylus tenuis	Prevalence (1, 2)	NS	None	NA
	Abundance (1)	<0.05	$Y_t = 1.03 + 0.264X_{t-1} - 0.129X_t$	0.6818
	Abundance (2)	<0.05	$Y_t = 0.477 + 0.251X_{t-1} + 0.183X_t$	0.6818
Cyrnea colini	Prevalence (1, 2)	NS	None	NA
	Abundance (1, 2)	<0.02	$Y_t = 0.636 + 0.020X_{t-1}$	0.4166
Cheilospirura spinosa	Prevalence (1, 2)	<0.005	$Y_t = 0.033 + 0.120X_{t-1}$	0.4820
	Abundance (1, 2)	<0.005	$Y_t = -0.084 + 0.084X_{t-1}$	0.5246
Tetrameres pattersoni	Prevalence (1, 2)	<0.005	$Y_t = 0.116 + 0.134X_{t-1}$	0.6016
	Abundance (1, 2)	<0.005	$Y_t = -0.082 + 0.123X_{t-1}$	0.6635
Raillietina cesticillus	Prevalence (1)	<0.005	$Y_t = -0.128 + 0.135X_{t-1}$	0.6465
	Prevalence (2)	<0.005	$Y_t = 0.039 + 0.135X_{t-1}$	0.6465
	Abundance (1)	<0.005	$Y_t = -0.291 + 0.154X_{t-1}$	0.5622
	Abundance (2)	<0.005	$Y_t = -0.070 + 0.154X_{t-1}$	0.5622
Raillietina colinia	Prevalence (1, 2)	<0.005	$Y_t = 0.564 - 0.110X_{t-1} + 0.156X_t$	0.3779
	Abundance (1, 2)	<0.005	$Y_t = 0.172 - 0.091X_{t-1} + 0.158X_t$	0.5824
Dispharynx nasuta	Prevalence (1, 2)	NS	None	NA
	Abundance (1, 2)	NS	None	NA
Aproctella stoddardi	Prevalence (1, 2)	NS	None	NA
	Abundance (1, 2)	NS	None	NA

[a] Study Sites 1 and 2 as described in text.

[b] Regression of helminth parasites on bobwhite density incorporating current year's bobwhite density (t subscript) and previous year's bobwhite density (t − 1 subscript) as covariate.

occurred prior to entrance of most juvenile bobwhites into the population in early summer. The timing of maximum transmission of *H. isolonche* prior to recruitment of young bobwhites suggests that worms present in bobwhites in February would have a high probability of being derived from eggs produced the preceding year. These features in the annual transmission of *H. isolonche* would produce the observed lag effect.

Trichostrongylus tenuis

The cecal worm, *T. tenuis*, has a monoxenous life cycle (Cram, 1927). Eggs are shed in feces, embryonate, hatch, and may result in infective larvae in as little as 2 days under optimum conditions (Cram et al., 1931). Prepatent periods in experimentally infected bobwhites have been as short as 4 days (Cram et al., 1931). Young bobwhites at TTRS have been found infected as early as July (Davidson et al., 1980). Studies have demonstrated a distinct winter (January to March) peak in acquisition of *T. tenuis* larvae by bobwhites at TTRS (Davidson et al., 1980; Moore et al., 1986), and *T. tenuis* is the predominant cecal nematode in bobwhites at TTRS in winter (Davidson et al., 1980). Bobwhites were the only known hosts for *T. tenuis* on TTRS until about 1980 when a small number of wild turkeys began frequenting the study sites.

Prevalence of *T. tenuis* was not related to bobwhite density on either study site (Table 4). As with *H. isolonche*, stable high prevalences (>72%) were maintained on both study sites (Fig. 2). Other studies (Kellogg and Prestwood, 1968; Davidson et al., 1980; Moore et al., 1986) also have found high prevalences of *T. tenuis* throughout the year at TTRS. Further, Forrester et al. (1984) reported more than 75% of the bobwhites examined from Leon County harbored *T. tenuis*. As postulated

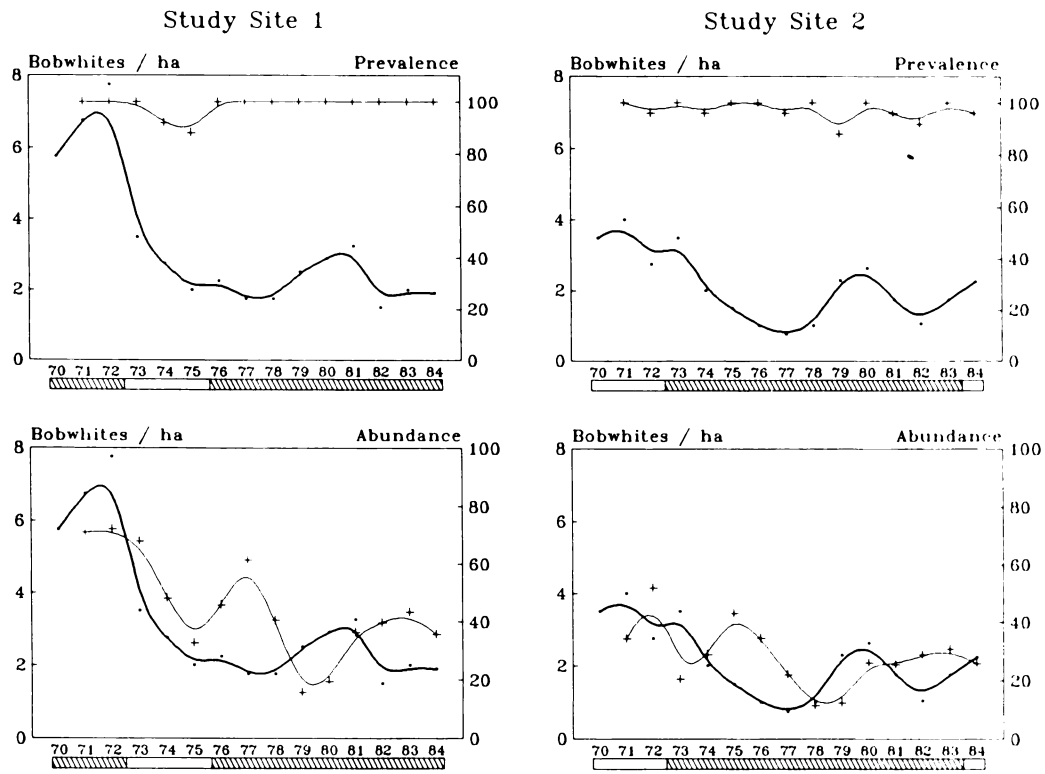

FIGURE 1. Comparison of the prevalence and abundance of *Heterakis isolonche* with bobwhite population density and agricultural field use on Study Sites 1 and 2 from 1971 to 1984. (Bobwhite density ●, *H. isolonche* +, Cultivation ▧, Fallow □.)

in regard to *H. isolonche*, the monoxenous life cycle of *T. tenuis* along with certain behavioral traits of bobwhites may combine to produce this stable high prevalence.

Similar to *H. isolonche*, abundance of *T. tenuis* was related to bobwhite density on both study sites (Table 4; Fig. 2), although in this latter instance the slopes and intercepts were different for the two sites (Table 4). Analyses further revealed that abundance of *T. tenuis* most closely fit a model that incorporated a combination of bobwhite density for both the previous year (lag effect) and the current year (Table 4). Assuming this to be a causal relationship, R^2 values suggest that approximately 68% of the variation in abundance was attributable to bobwhite density.

Appearance of current year's bobwhite density as a covariate in the regression equation suggests that many *T. tenuis* were derived from infective larvae produced after entrance of juvenile bobwhites into the population (i.e., within-year transmission). Moore et al. (1986) recently demonstrated a distinct winter peak in acquisition of *T. tenuis* larvae by TTRS bobwhites that was followed by a peak in adult *T. tenuis*. Moore et al. (1986) further noted that, although *T. tenuis* potentially could have rapid, year-round transmission, it is a seasonally occurring parasite. We suggest that the seasonal timing of transmission affords an explanation for the relationship to the current year's bobwhite density.

Trichostrongylus tenuis predominates during cooler seasons whereas *H. isolonche*, the only other monoxenous parasite, predominates during the warmer seasons (Davidson et al., 1980; Moore et al., 1986). Studies on wild turkeys in south-central Florida also showed a winter peak of *T. tenuis* (Hon et al., 1978). Collective-

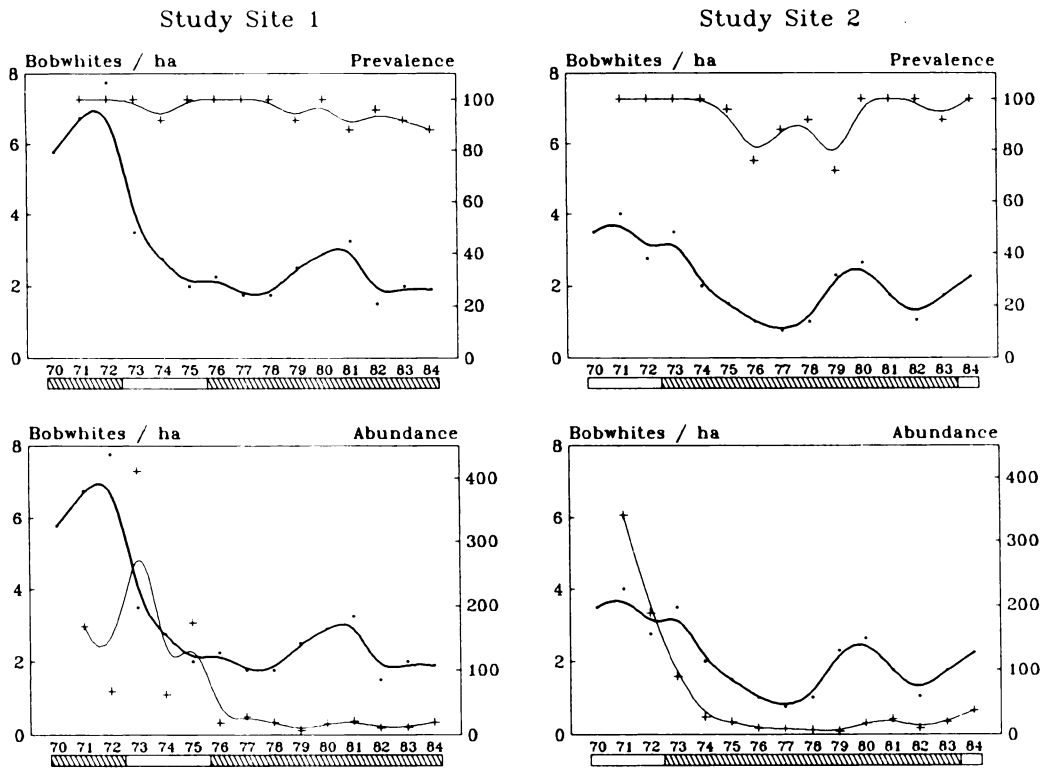

FIGURE 2. Comparison of the prevalence and abundance of *Trichostrongylus tenuis* with bobwhite population density and agricultural field use on Study Sites 1 and 2 from 1971 to 1984. (Bobwhite density ●, *T. tenuis* +, Cultivation ▧, Fallow □.)

ly, these findings suggest a generally occurring phenomenon of seasonality by *T. tenuis* in wild galliform hosts in Florida. Moore et al. (1986) have postulated that this seasonality may reflect vulnerability to abiotic climatic factors, for example desiccation of larvae during hot summer months.

Of interest in this regard were higher ($P \leq 0.01$) abundances of *T. tenuis* during years when agricultural fields were fallow (Table 5; Fig. 2). Although unproven by experimental study, we suggest that some or all of the factors below enhance development, survival, and transmission of *T. tenuis* in fallow fields. First, bobwhites readily utilize fallow fields throughout the year, but they curtail use of corn fields following harvest, presumably due to inadequate overhead cover. Second, the light covering of litter on fields fallow for three or fewer years would be a minimal physical barrier between larvae and bobwhites. Most of the woodland portions of the study sites support dense stands of grasses and forbs due to annual controlled burning. This dense mat of vegetation in woodlands may function as a physical barrier suppressing transfer of larvae. Third, the screening effect of weedy vegetation (approximately 0.5 m to 2 m high and virtually 100% coverage) in fallow fields would reduce ground surface temperatures and increase ground level humidity. These conditions would favor development of eggs and larvae and would improve survival of larvae during October and November which are typically hot and dry at TTRS. Fourth, most eggs and larvae at the ground surface probably are eliminated when the fields are cultivated. Thus, although agricultural fields comprised only about 20% of each study site, we hypothesize that certain attributes of fallow fields

TABLE 5. Comparison of transformed mean prevalence and abundance for common species of helminths in bobwhites during years when fields were cultivated versus when fields were fallow.[a]

Species	Parameter	Cultivated	Fallow	*P*
Heterakis isolonche	Abundance	1.5874	1.6615	0.6096
Trichostrongylus tenuis	Abundance	1.6644	2.1904	0.0143
Cyrnea colini	Prevalence	1.2500	1.3170	0.4004
	Abundance	0.6981	0.7426	0.2510
Cheilospirura spinosa	Prevalence	0.4499	0.7807	0.0098
	Abundance	0.1850	0.4602	0.0121
Tetrameres pattersoni	Prevalence	0.6586	0.7916	0.2604
	Abundance	0.4318	0.4745	0.7331
Raillietina cesticillus	Prevalence	0.4348	0.5756	0.5086
	Abundance	0.3749	0.5131	0.5708
Raillietina colinia	Prevalence	0.7716	0.5429	0.0320
	Abundance	0.4324	0.2959	0.0239

[a] Prevalence data arcsin transformed and intensity data log transformed as described in text; analyses omitted if prevalence approximated 100% (i.e., *H. isolonche* and *T. tenuis*) or if data were insufficient (i.e., *A. stoddardi* and *D. nasuta*); bobwhite density included as a covariate; for years 1971 to 1975 and 1984 only.

and their attendant influences on bobwhite behavior interact to produce an important nidus for transmission of *T. tenuis*.

Cyrnea colini

Cyrnea colini, which parasitizes the proventricular-gizzard isthmus, has a heteroxenous life cycle with several species of galliform birds as definitive hosts (Cram, 1931a; Davidson et al., 1977b). Experimental studies have demonstrated that cockroaches (*Blatella germanica*) and possibly grasshoppers (*Chortophaga viridifasciata*) are suitable intermediate hosts; however, the major intermediate host(s) in nature are unknown (Cram, 1931a, 1934b). Larva-containing eggs passed in feces develop to the infective third-stage in 18 to 45 days when ingested by cockroaches (Cram, 1931a). The prepatent period is unknown, although fourth stage larvae and "immature adults" occurred in the proventriculus at 13 days post-infection, and fully developed adults were found at 41 days (Cram, 1931a). Young bobwhites at TTRS harbored *C. colini* by July, and by January prevalence and intensity in juvenile bobwhites were equivalent to those values for adults (Davidson et al., 1980). The major period of transmission at TTRS, as indicated by the presence of immature *C. colini* in bobwhites, extended from June through December with a peak in July–August (Davidson et al., 1980). Bobwhites were the only known definitive host for *C. colini* at TTRS until about 1980 when a small number of wild turkeys began to frequent the sites.

Prevalence of *C. colini* was not related to bobwhite density on either study site (Table 4). Stable high prevalences (≥80%) were maintained on both study sites (Fig. 3). Other studies (Kellogg and Prestwood, 1968; Davidson et al., 1980; Moore et al., 1986) also revealed relatively high prevalences (50 to 100%) of *C. colini* throughout the year at TTRS. Forrester et al. (1984) reported a 95% prevalence of *C. colini* in bobwhites from Leon County and an overall 72% prevalence in bobwhites from six areas in Florida. Although *C. colini* is heteroxenous, it apparently has a highly efficient life cycle. One factor may be that, compared to other heteroxenous species, the relatively long period of transmission of *C. colini* provides increased opportunity for infection. Immature *C. colini*, which were presumed to represent recently acquired infections, made up more than 10% of all *C. colini* detected in bobwhites from June–December, and at least some immature worms were found during 10 of

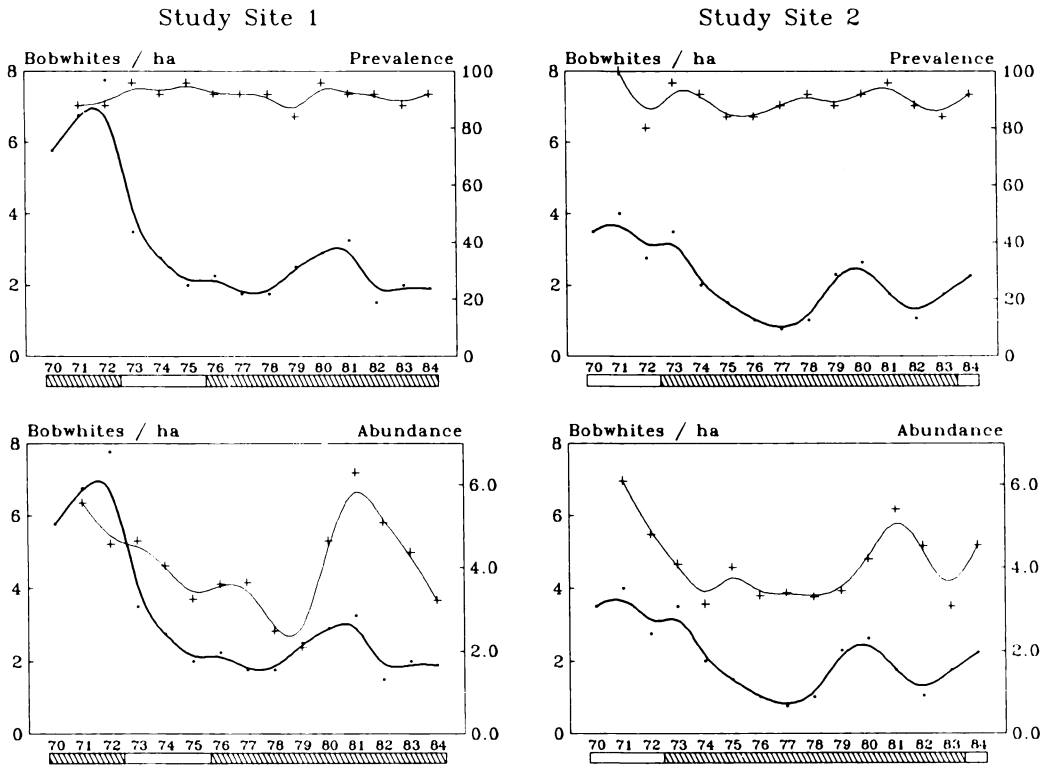

FIGURE 3. Comparison of the prevalence and abundance of *Cyrnea colini* with bobwhite population density and agricultural field use on Study Sites 1 and 2 from 1971 to 1984. (Bobwhite density ●, *C. colini* +, Cultivation ▧, Fallow □.)

12 mo that bobwhites were examined (Davidson et al., 1980).

In contrast to prevalence, abundance of *C. colini* was related to bobwhite density on both study sites (Table 4; Fig. 3). Again assuming a causal relationship, R^2 values suggest that approximately 42% of the variability in abundance was attributable to bobwhite density (Table 4). We believe this relationship is causal because bobwhites were the only definitive host for *C. colini* at TTRS. Variation in intermediate host population density also would be expected to influence heteroxenous species, however, either confounding or accentuating the influence of definitive host densities. Analyses indicated that abundance most closely fit a model that incorporated bobwhite density for the preceding February (Table 4); thus, abundance tended to exhibit a 1 yr lag effect. A possible factor contributing to this is that acquisition of *C. colini* peaks in July–August, although limited transmission continues through December (Davidson et al., 1980). Thus, the majority of infective stages would be derived before recruitment of juvenile bobwhites had established the current year's bobwhite density.

Cheilospirura spinosa

The gizzard worm, *C. spinosa*, has a heteroxenous life cycle involving several species of galliform birds as definitive hosts and grasshoppers (*Melanoplus femurrubrum, M. differentalis*) as experimental intermediate hosts (Cram, 1929, 1931a). Larvated eggs are passed in feces and when consumed by intermediate hosts, develop to infective larvae within 25 days (Cram, 1931a). Prepatent periods are 32 to 45 days in experimentally infected bobwhites, and parasite longevity can be at least 84 days (Cram, 1931a). Young bobwhites at TTRS

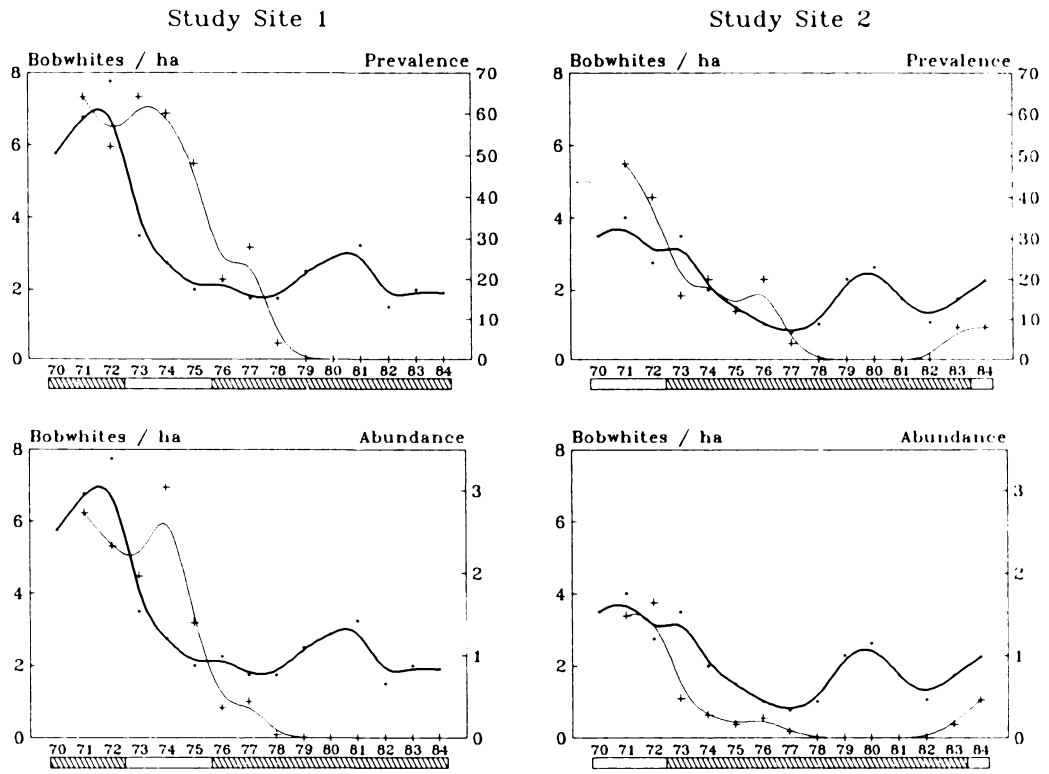

FIGURE 4. Comparison of the prevalence and abundance of *Cheilospirura spinosa* with bobwhite population density and agricultural field use on Study Sites 1 and 2 from 1971 to 1984. (Bobwhite density ●, *C. spinosa* +, Cultivation ▧, Fallow □.)

had acquired infections of immature *C. spinosa* by July, and by January prevalence and intensity in juvenile bobwhites approached those values for adults (Davidson et al., 1980).The period of transmission at TTRS, as indicated by the presence of immature *C. spinosa* in bobwhites, was almost totally restricted to the 3-mo-period of July–September (Davidson et al., 1980). Bobwhites were the only known definitive hosts for *C. spinosa* at TTRS until about 1980, when a small number of wild turkeys began to frequent the sites.

Both prevalence and abundance of *C. spinosa* were related to bobwhite density on each study area (Table 4; Fig. 4). Assuming a causal relationship, R^2 values indicated that approximately 48% of the variability in prevalence and 52% of the variability in abundance were attributable to bobwhite density (Table 4). Bobwhite populations on both study sites generally were at their lowest levels from 1975-1978, and during these consecutive years of low bobwhite density, *C. spinosa* declined markedly (Fig. 4). From 1979 to 1982, *C. spinosa* was not detected on either study site suggesting that temporarily it became locally extinct or at least was very rare. The data strongly suggest that a major factor in the decline of *C. spinosa* was the sustained low density of bobwhites. This hypothesis is probable since bobwhites were the only definitive host at TTRS. Furthermore, *C. spinosa* has a rather restricted period of transmission (Davidson et al., 1980) which may make it more vulnerable to low definitive host densities.

Prevalence and abundance of *C. spinosa* most closely fit models that incorporated only bobwhite density for the preceding February (Table 4); thus, *C. spinosa* exhibited a 1-yr lag effect. A potential factor that could produce a lag effect is the

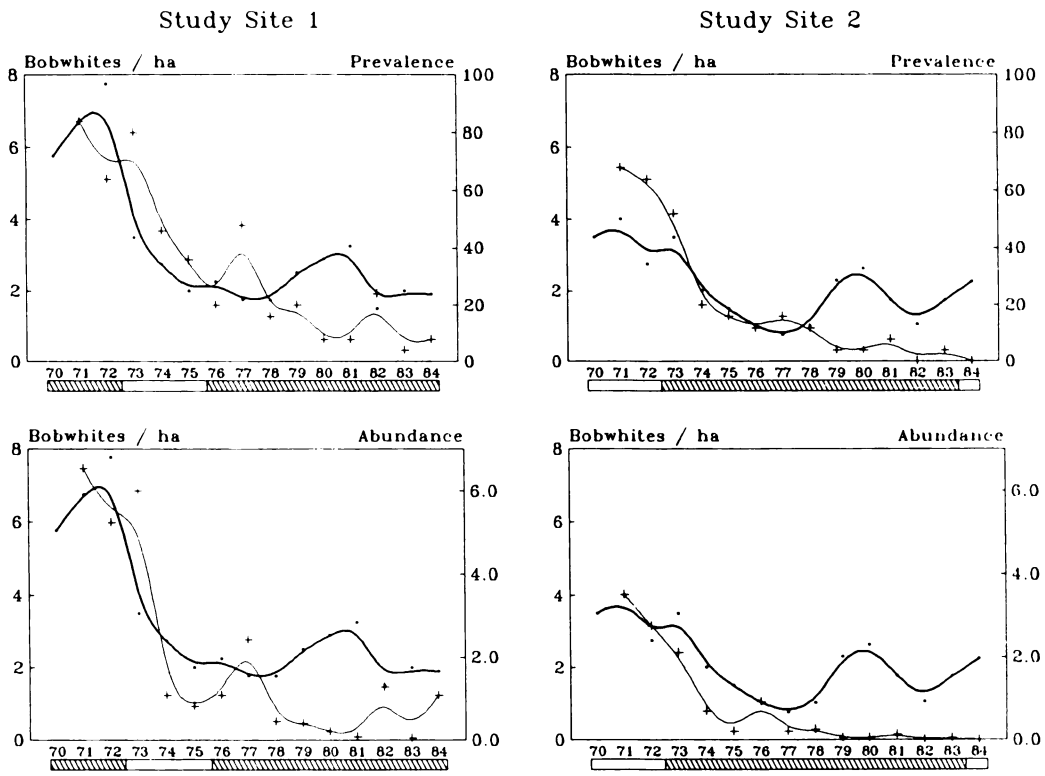

FIGURE 5. Comparison of the prevalence and abundance of *Tetrameres pattersoni* with bobwhite population density and agricultural field use on Study Sites 1 and 2 from 1971 to 1984. (Bobwhite density ●, *T. pattersoni* +, Cultivation ▧, Fallow □.)

asynchrony of the peaks of transmission and the recruitment of juvenile bobwhites into the population. The peak transmission of *C. spinosa* (Davidson et al., 1980) occurred shortly after the typical period of peak bobwhite recruitment (Stoddard, 1931), and thus would increase the probability that infective stages were derived from eggs shed by the preceding year's bobwhite population.

Prevalence and abundance of *C. spinosa* were higher ($P \leq 0.01$) when agricultural fields were fallow (Table 5; Fig. 4). The importance of this variable is evident when it is noted that changes in field status apparently were more critical than host density in determining the abundance of *C. spinosa*. For example, the prevalence, but also to some extent the abundance, of *C. spinosa* declined on both study sites the first year after fallow fields were returned to cultivation even though bobwhite densities on both sites increased (Fig. 4). Further, even though bobwhite density declined by more that half when fields on Study Site 1 were fallowed in 1973, prevalence and abundance of *C. spinosa* showed slight increases (Fig. 4). These findings suggest that some component of the fallow field community, perhaps a major intermediate host species, is particularly important to the perpetuation of *C. spinosa*.

Tetrameres pattersoni

The proventricular nematode, *T. pattersoni*, has a heteroxenous life cycle involving bobwhites as the only known definitive host and cockroaches (*B. germanica*) and grasshoppers (*M. femurrubrum* and *C. viridifasciata*) as experimental intermediate hosts (Cram, 1930, 1931b, 1934a). Eggs containing larvae are passed in feces and develop to infective

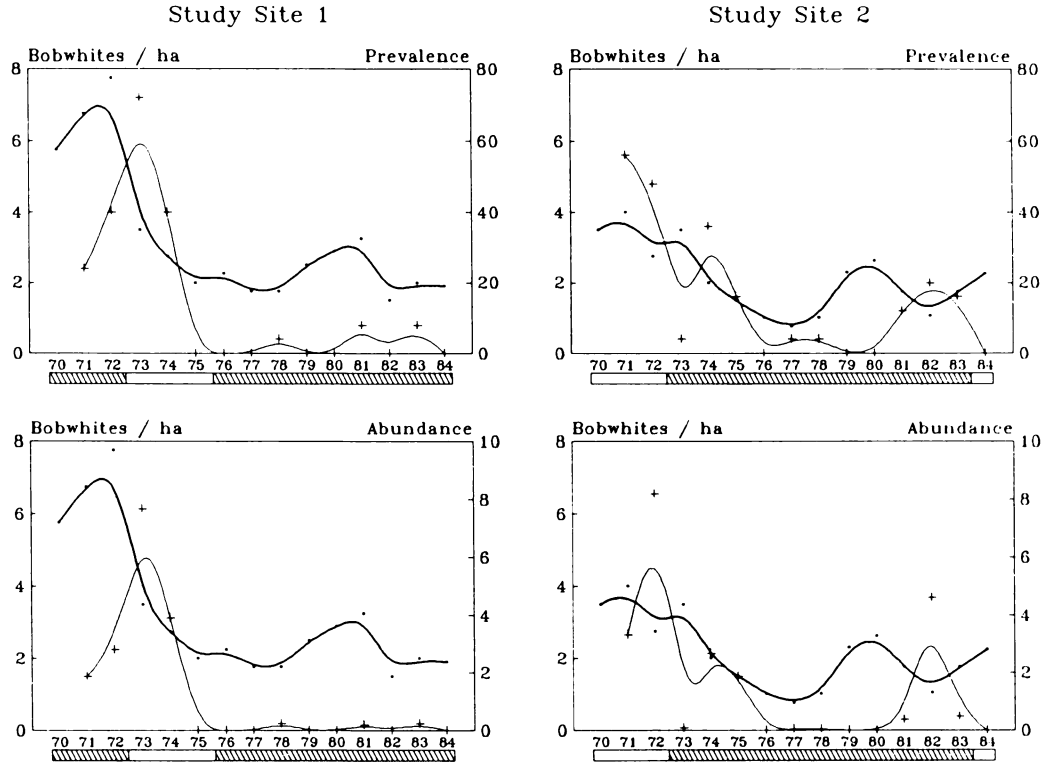

FIGURE 6. Comparison of the prevalence and abundance of *Raillietina cesticillus* with bobwhite population density and agricultural field use on Study Sites 1 and 2 from 1971 to 1984. (Bobwhite density ●, *R. cesticillus* +, Cultivation ▧, Fallow □.)

larvae within 24 days when consumed by grasshoppers (Cram, 1934a). Prepatent and patent periods are unknown, as is longevity of the parasite. Young bobwhites at TTRS had acquired infections of *T. pattersoni* by July, and by January prevalence and intensity in juvenile bobwhites was equivalent to those values for adults (Davidson et al., 1980). The period of transmission at TTRS, as indicated by the presence of immature *T. pattersoni* in bobwhites, was almost totally restricted to a 2-mo period in June and July (Davidson et al., 1980).

Both prevalence and abundance of *T. pattersoni* were related to bobwhite density on each study area (Table 4). Assuming a causal relationship, R^2 values indicated that approximately 60% of the variability in prevalence and 66% of the variability in abundance were attributable to bobwhite density. Prevalence and abundance of *T. pattersoni* most closely fit models that incorporated only bobwhite density for the preceding February (Table 4); thus, *T. pattersoni* exhibited a 1-yr lag effect. Annual trends in prevalence and abundance of *T. pattersoni* on each site (Fig. 5) were remarkably similar to those of *C. spinosa* (Fig. 4). Similarities in the life cycles of these two species, such as utilization of the same species of grasshoppers as intermediate hosts and brief synchronized peaks of transmission in summer (Davidson et al., 1980; Moore et al., 1986), may be important factors in producing the parallel trends noted between these species. In fact, the occurrence of *C. spinosa* and *T. pattersoni* in individual bobwhites was not independent ($\chi^2 = 16.8$; df = 1). This association may be attributable to the use of the same species as intermediate hosts, or alternatively that individual intermediate hosts frequently have dual infections with larvae of both species.

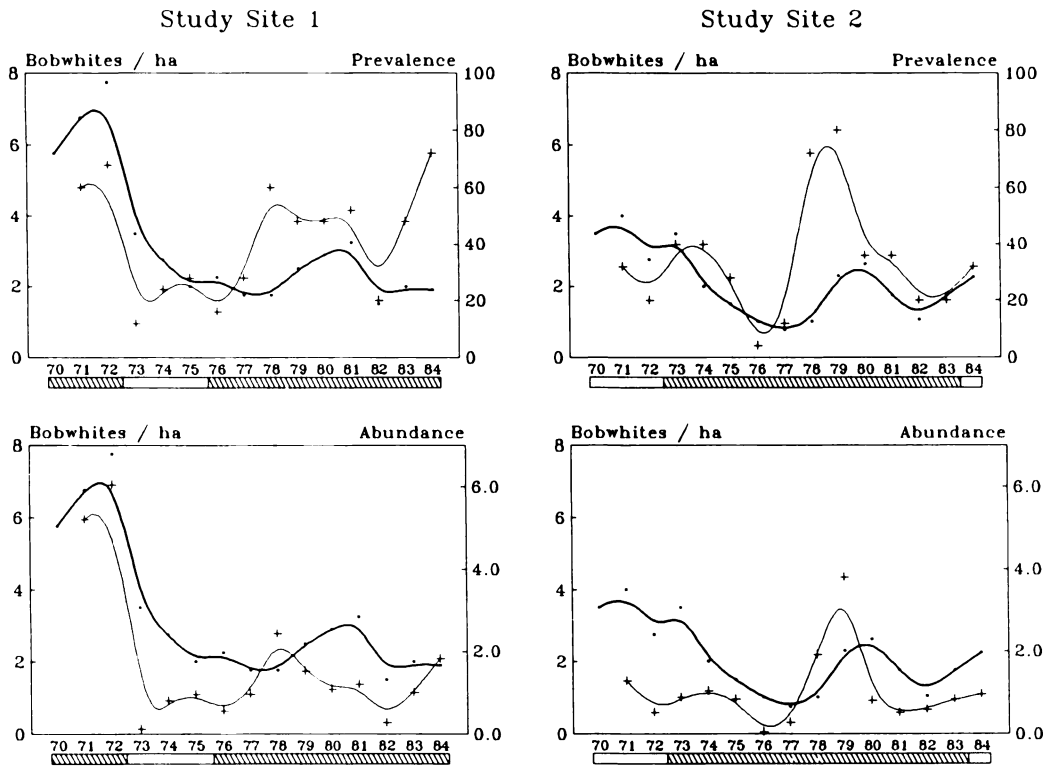

FIGURE 7. Comparison of the prevalence and abundance of *Raillietina colinia* with bobwhite population density and agricultural field use on Study Sites 1 and 2 from 1971 to 1984. (Bobwhite density ●, *R. colinia* +, Cultivation ▧, Fallow □.)

Although similar in the above respects, *T. pattersoni* and *C. spinosa* differ with regard to other factors. In contrast to *C. spinosa*, there was no indication that cultivation of agricultural fields had any relationship to the occurrence of *T. pattersoni* (Table 5). Additionally, *T. pattersoni* is widely distributed in bobwhites in Florida whereas *C. spinosa* has been reported only from Leon County (Forrester et al., 1984; Cram et al., 1931).

Raillietina cesticillus

The tapeworm, *R. cesticillus*, has a heteroxenous life cycle involving several species of galliform birds as definitive hosts and over 100 species of beetles as intermediate hosts (Reid, 1962). Proglottids containing onchospheres are shed in feces and develop into cysticercoids in beetles within as few as 14 days (Reid, 1962). The prepatent period may be as short as 13 days, and parasite longevity as much as 18 mo (Reid, 1962). Young bobwhites at TTRS have been found infected as early as August (Davidson et al., 1980); however, infections of *R. cesticillus* in juveniles tended to appear later than infections of other common species (Davidson et al., 1980; Moore et al., 1986). Neither peaks in transmission nor seasonal trends in infections were evident in bobwhites from TTRS (Davidson et al., 1980; Moore et al., 1986). Bobwhites were the major definitive host on the study sites, although a small flock of free-ranging, domestic chickens (*Gallus gallus*) occasionally ventured onto small portions of both study sites until about 1975. In 1970, this flock of chickens was infected with *R. cesticillus* (G.L. Doster, unpubl. data).

Both prevalence and abundance of *R. cesticillus* were related to bobwhite density; however, regression intercepts and

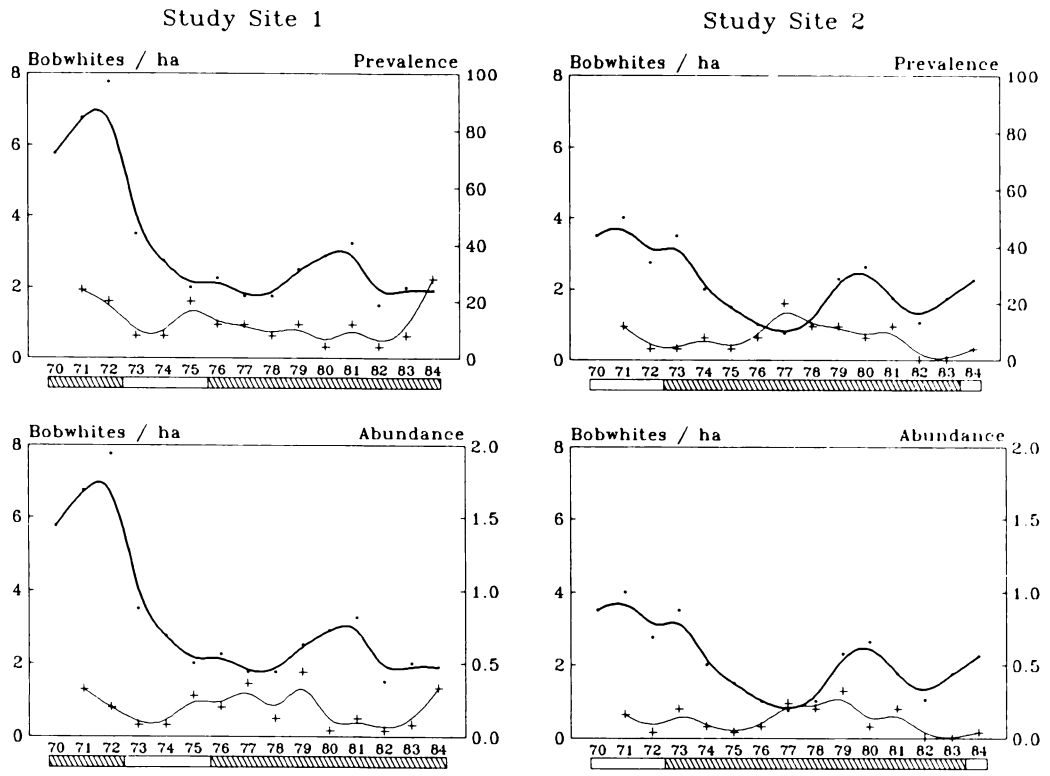

FIGURE 8. Comparison of the prevalence and abundance of *Dispharynx nasuta* with bobwhite population density and agricultural field use on Study Sites 1 and 2 from 1971 to 1984. (Bobwhite density ●, *D. nasuta* +, Cultivation ▧, Fallow □.)

slopes differed between the two study sites (Table 4). Prevalence and abundance of *R. cesticillus* best fit models that incorporated only the previous year's bobwhite density (Table 4). Assuming a causal relationship, R^2 values indicated that approximately 65% of the variability in prevalence and 56% of the variability in abundance were attributable to bobwhite density. Although related to bobwhite density, the occurrence of *R. cesticillus* exhibited erratic fluctuations during the course of the study (Fig. 6). Erratic fluctuations also were evident during studies of seasonal trends of parasitism in bobwhites at TTRS (Davidson et al., 1980; Moore et al., 1986). Factors involved in these fluctuations are not known.

Raillietina colinia

The tapeworm, *R. colinia*, has a heteroxenous life cycle with bobwhites as the only reported definitive host (Webster, 1944; Webster and Addis, 1945; Davidson et al., 1980, 1982; Moore et al., 1986). Intermediate hosts and other aspects of the life cycle are unknown. Juvenile bobwhites at TTRS had acquired infections of *R. colinia* by July, and thereafter infections in juveniles equaled or exceeded those in adults (Davidson et al., 1980). Neither discernible peaks in transmission nor seasonal trends in infection were evident in bobwhites from TTRS (Davidson et al., 1980; Moore et al., 1986).

Both prevalence and abundance of *R. colinia* were related to bobwhite density on each study site (Table 4). Prevalence and abundance of *R. colinia* best fit models that incorporated both preceding and current year's bobwhite densities (Table 4). Assuming a causal relationship, R^2 values indicated that approximately 38% of the variability in prevalence and 58% of the

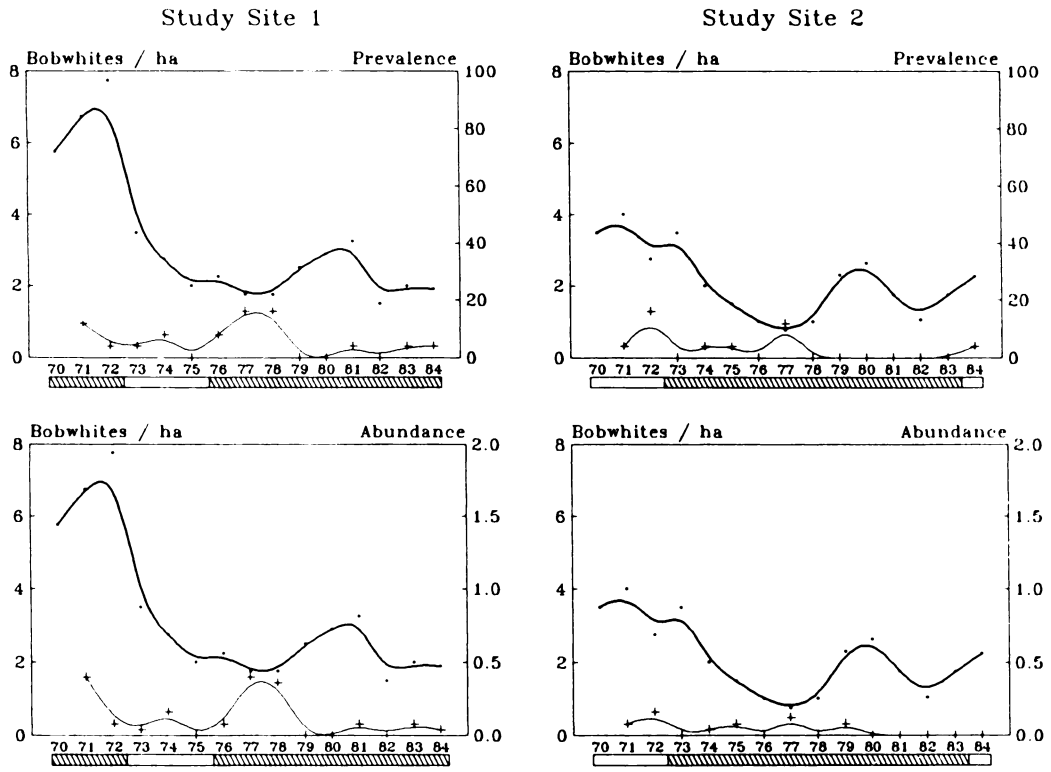

FIGURE 9. Comparison of the prevalence and abundance of *Aproctella stoddardi* with bobwhite population density and agricultural field use on Study Sites 1 and 2 from 1971 to 1984. (Bobwhite density ●, *A. stoddardi* +, Cultivation ▧, Fallow □.)

variability in abundance were attributable to bobwhite density (Table 4). Prevalence and abundance of *R. colinia* were higher ($P < 0.05$) when agricultural fields were cultivated (Table 5; Fig. 7) suggesting that this activity enhanced opportunity for transmission, possibly by influencing abundance or availability of an important intermediate host. Despite the relationships to bobwhite density and agricultural field status, *R. colinia* exhibited dramatic and unexplained increases on both study sites in 1978 indicating that other factors also are important determinants of its abundance.

Dispharynx nasuta

The proventricular worm, *D. nasuta*, has a heteroxenous life cycle involving numerous genera and species of birds as definitive hosts and several genera of isopods (*Armadillidium*, *Chaetophiloscia*, *Venezillo*, *Oscelloscia*, and *Porcellio*) as intermediate hosts (Cram, 1931a; Hon et al., 1978; Rickard, 1985). Eggs containing larvae are passed in feces and develop to the infective stage in isopods within 26 days (Cram, 1931a). The prepatent period in experimentally infected bobwhites is 27 days (Cram, 1931a); however, the patent period and parasite longevity in bobwhites are unknown. *Dispharynx nasuta* tends to be more abundant in younger birds (Goble and Kutz, 1945; Bendell, 1955; Hon et al., 1978; Rickard, 1985), and young juvenile bobwhites at TTRS have higher prevalences of *D. nasuta* than adults (Davidson et al., 1980; Moore et al., 1986). Neither peak periods of transmission nor seasonal trends in abundance were evident in bobwhites at TTRS (Davidson et al., 1980; Moore et al., 1986).

Neither prevalence nor abundance of *D. nasuta* were related to bobwhite density

on either study site (Table 4). Stable low prevalences (≤29%) and abundances (≤1 worm) occurred throughout the study despite the 10-fold difference in bobwhite density (Fig. 8). Forrester et al. (1984) reported similar low prevalences and intensities of *D. nasuta* in bobwhites from Leon and five other counties in Florida. *Dispharynx nasuta* has been reported from a variety of avian species that cohabit the study sites with bobwhites (Barrows and Hayes, 1977; Cooper and Crites, 1976; Hon et al., 1978; Rickard, 1985). This broad range of hosts apparently acts as a buffer preventing fluctuations in the density of any single definitive host species, bobwhites in this instance, from markedly influencing the abundance. Hon et al. (1978) similarly suggested the importance of a broad range of definitive hosts in the maintenance of *D. nasuta* infections among wild turkeys in Florida.

Aproctella stoddardi

Aproctella stoddardi, which inhabits the body cavity, air sacs, pericardial sac, and occasionally other organs, is a filarial nematode capable of infecting many genera and species of birds (Anderson, 1957, 1961; Cram et al., 1931; Forrester et al., 1983; Barrows and Hayes, 1977). Microfilariae occur in the blood, but the presumed hematophagus intermediate host(s) are unknown. Periods of transmission and other details of the ecology of *A. stoddardi* in bobwhites at TTRS are unknown.

Neither prevalence nor abundance of *A. stoddardi* were related to bobwhite density on either study site (Table 4). Stable low prevalences (≤16%) and abundances (≤1 worm) occurred throughout the study despite the 10-fold difference in bobwhite density (Fig. 9). Forrester et al. (1984) also found a low prevalence and intensity of *A. stoddardi* in bobwhites from Leon County. The wide range of definitive hosts of *A. stoddardi* may act as a buffer, as was postulated for *D. nasuta*.

ACKNOWLEDGMENTS

This study was supported in part by Tall Timbers Research, Inc., Tallahassee, Florida and in part by the Federal Aid in Wildlife Restoration Act (50 Stat. 917) and through Contract Numbers 14-16-0008-676, 14-16-0008-2029, 14-16-0009-78-024, 14-16-0009-82-500, 14-16-0004-83-004, and 14-16-0004-84-005, Fish and Wildlife Service, U.S. Department of the Interior. This work would not have been possible without the encouragement and assistance of personnel at Tall Timbers Research Station, especially E. V. Komarek, Sr., Roy Komarek, Leon Neel, Bruce Means, Jimmy Atkinson, and Leroy Collins. The help of many co-workers, biologists, student volunteers, and other colleagues over the years with the long hours of field work during this study also is gratefully acknowledged. Thanks are also due Don Hayne, Ken Pollock, and David Turner, Southeastern Cooperative Wildlife and Fisheries Statistics Project, North Carolina State University for assistance with statistical analyses. We thank D. J. Forrester for many helpful suggestions during preparation of this manuscript.

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Received for publication 29 August 1989.