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ABSTRACT: Nine species of helminths, all nematodes, were recovered from the viscera of 48 feral swine (*Sus scrofa*) from Cumberland Island, Georgia. Both the overdispersed frequency distributions and the abundances of the four common species of helminths (*Stephanurus dentatus, Metastrongylus apri, M. pudendotectus* and *Gongylonema pulchrum*) did not vary significantly across the main and interactive effects of host sex and/or seasons. Whether or not the present low population densities of feral swine on Cumberland Island has influenced the pattern of fluctuations in abundances of helminth species across seasons as often observed in helminth communities from other hosts was not resolved. The apparent recent decline in prevalences and abundances, and the loss of certain species from the helminth communities of feral swine on the island may be explained partially by the decreasing transmission potentials of direct life cycle species caused by a recent marked reduction of numbers of individuals in the host population. Conversely, the apparent increased prevalence and abundance of three species of helminths (*S. dentatus, M. apri* and *M. pudendotectus*) may be related to their common utilization of earthworms as paratenic or intermediate hosts. *Gongylonema pulchrum* was the only helminth in which abundances seemed to remain unchanged. This was the only species that was not strictly host specific to feral swine. We found no evidence that helminth infections were responsible for morbidity or mortality in this feral swine population.

Key words: Feral swine, *Sus scrofa*, nematodes, helminth communities, ecology, overdispersion, distribution patterns, season, host sex.

INTRODUCTION

The helminth fauna of populations of feral swine (*Sus scrofa*) in the southeastern United States has been investigated extensively (Babero et al., 1959; Hanson and Karstad, 1959; Henry and Conley, 1970; Foreyt and Todd, 1972; Coombs and Springer, 1974; Prestwood et al., 1975; Ruddle, 1975; Smith, 1981; Smith et al., 1982). However, most of these studies involved single collections of small host sample sizes and were concerned principally with species composition and prevalence.

Although previous studies included data on prevalence of helminths from insular populations of feral swine from Ossabaw Island (Prestwood et al., 1975) and Cumberland Island (Smith, 1981; Smith et al., 1982), Georgia, a recent reduction in the feral swine population on Cumberland Island initiated by the National Park Service allowed access to additional data for a more extensive examination of the helminth communities of this host. Thus, the objectives of our study were to (1) re-examine the species composition and abundances of species in the helminth communities of an insular population of feral swine that had experienced a recent population reduction and (2) determine the effects of selected host and seasonal variables on the structure of the helminth community in this host population.

MATERIALS AND METHODS

Study area

Cumberland Island is approximately 25 × 1 to 9 km (about 9,400 ha, including salt marshes) and is separated by a linear distance of about 2 km from the mainland by the Cumberland River and Cumberland Sound (Hillestad et al., 1975). It is located in Camden County, Georgia at 30°48′N latitude and 81°26′W longitude. The climate is classified as humid subtropical with normal mean temperatures ranging from 12 C in December and January to 28 C in July and August (Johnson et al., 1974). There is an average of 305 freeze-free days, and the average minimum temperature in January is 6 C (Johnson et al., 1974). Mean annual precipitation is

137 cm with more than one-half occurring from June to September (Plummer, 1983).

The principal natural plant communities on the island include dune, interdune flats, salt marsh, freshwater and upland forests (Hillestad et al., 1975). The dune and interdune flats represent about 15% of the island's area and are characterized primarily by various grasses and forbs with shrubs, live oak (*Quercus virginianus*) and pines (*Pinus* spp.) on higher sites. About 37% of the island is salt marsh which is dominated almost entirely by smooth cordgrass (*Spartina alterniflora*) with various forbs, shrubs and live oak on higher sites. Freshwater communities include lakes, ponds and sloughs characterized by various aquatic plants with some shrubs and lowland mixed hardwoods. They comprise about 8% of the island's area. Approximately 39% of the island is upland forest characterized by various forbs, shrubs and vines in the understory and hardwoods (mostly live oaks), broad-leaved evergreens and pines in the overstory (Hillestad et al., 1975).

Originally under private ownership, Cumberland Island was designated a National Seashore and incorporated into the National Park System in 1972. During the past 10–20 yr, the island was inhabited by "several hundred" feral swine and feral cattle, and lesser numbers of feral horses and white-tailed deer (*Odocoileus virginianus*) (Hillestad et al., 1975). All feral cattle were removed in 1975. In late 1975 a program was instituted to remove feral swine, but the major removal work did not occur until the late 1970's and early 1980's (K. O. Morgan, pers. comm.). Records for a live-trapping and removal program from 1975 to 1983 and hunter-killed removals from 1983 to 1985 document an estimated reduction, inclusive of recruitment, in the feral swine population of at least 1,700 individuals (K. O. Morgan, pers. comm.).

Data collection

Eight collections of adult (≥1 yr old) feral swine were made at 2–3-mo intervals from October 1984 through June 1986. We collected feral swine by shooting. Samples were obtained also from hunter-killed feral swine. A total of 20 male and 28 female feral swine was collected and examined.

Within 12 hr after death animals were eviscerated. The esophagus, trachea, and colon were ligated and the viscera were frozen until later necropsy. In general, necropsy techniques followed the procedures outlined by Samuel (1979) and Wobeser and Spraker (1980), except visual examination of gastrointestinal contents was supplemented by repeated washing and sedimentation in conical glasses and the sediment was examined with a stereomicroscope. Feral swine were not examined for helminths residing in locations other than the thoracic and abdominal viscera.

Nematodes were fixed briefly in glacial acetic acid, stored in a mixture of 70% ethyl alcohol with 5% glycerine, and examined in glycerine wet mounts. Representative specimens of the helminth species collected in this study are deposited in the U.S. National Parasite Collection, Beltsville, Maryland 20705, USA (Nos. 79812–79820).

Definitions

The terms prevalence, intensity, mean intensity and abundance follow the definitions of Margolis et al. (1982). Overdispersion as defined by Bliss and Fisher (1953) was used herein for helminth frequency distributions as defined by Corn et al. (1985). The terms significant and significantly refer to statistical significance at $P \leq 0.05$. Common species of helminths are defined as those occurring at ≥20% prevalence in the host population. Based on temperature and precipitation patterns, individual collections of feral swine were pooled into warm and cool season collections for subsequent analyses. The warm and cool seasons included the months of April through October and November through March, respectively. A period of at least 6 wk separated the last collection of one season from the first collection of the next season.

Data analysis

Overdispersion was indicated when the variance was significantly larger than the mean in the frequency distribution of the respective parasite species by chi-square analysis and was defined by the negative binomial parameter, k (Bliss and Fisher, 1953). Homogeneity in the values of k generated from the common helminth species' frequency distributions across host and seasonal variables were calculated by the method outlined in Wallace and Pence (1986) as modified from Bliss and Fisher (1953).

Since the frequency distributions of the common species of helminths were highly overdispersed, their abundance values were rank transformed by the procedure of Conover and Iman (1981) prior to subsequent analysis (PROC RANK; Statistical Analysis Systems, 1985, SAS Institute Inc., Cary, North Carolina 27511, USA). The main and interactive effects of the two independent variables of host sex and season were examined with a factorial ANOVA for each of the four common species of helminths (dependent variables) and subsequently with a MANOVA for the collective helminth fauna (four common species collectively) (PROC GLM; SAS). Three combinations of factors potentially influencing the abundances of individual species

TABLE 1.   Visceral helminths of an insular population of feral swine from Cumberland Island, Georgia.

Species of helminth[a]	Prevalence		Intensity		Abundance	
	Infected/ examined	%	$\bar{x} \pm SE$[b]	Range	$\bar{x} \pm SE$	Total
Stephanurus dentatus (K, M)	26/48	54	19.3 ± 3.6	1–65	10.2 ± 2.3	488
Metastrongylus apri (L)	36/48	75	25.2 ± 4.4	1–114	18.9 ± 3.7	906
Metastrongylus pudendotectus (L)	17/48	35	9.9 ± 3.8	1–61	3.5 ± 1.5	169
Globocephalus urosubulatus (SI)	2/48	4	20.0 ± 10.0	10–30	0.8 ± 0.7	40
Oesophagostomum quadrispinulatum (LI, C)	2/48	4	283.0 ± 158.0	125–440	11.7 ± 9.4	565
Ascaris suum (SI, LI)	6/48	13	1.7 ± 0.5	1–4	0.2 ± 0.1	10
Gongylonema pulchrum (E, L)	37/48	77	7.4 ± 1.2	1–29	5.5 ± 1.0	266
Physocephalus sexalatus (S, SI)	6/48	13	55.0 ± 28.5	5–185	6.9 ± 4.2	330
Ascarops strongylina (S)	3/48	6	26.7 ± 19.2	5–65	1.7 ± 1.4	80

[a] C, caecum; E, esophagus; K, kidney; L, lung; LI, large intestine; M, mesenteries; S, stomach; SI, small intestine.
[b] Mean ± standard error.

of helminths and the collective fauna were possible (host sex, season, and host sex × season).

RESULTS

Nine species of helminths, all nematodes, were recorded from 48 adult feral swine for the 1½-yr period of collection from Cumberland Island. Data on prevalence, intensity and abundance are listed in Table 1. All these helminths have been reported previously from feral swine in the southeastern United States (Smith et al., 1982).

All hosts were infected with 1–4 ($\bar{x}$ = 2.8) species of helminths. There were 1 (2%), 18 (38%), 17 (36%), and 11 (24%) of the swine with 1, 2, 3 and 4 species of helminths, respectively. A total of 2,843 helminth individuals were recovered from the 48 swine. Intensities ranged from 1 to 440 ($\bar{x}$ = 59.2).

For each of the four common species of helminths (Stephanurus dentatus, Metastrongylus apri, M. pudendotectus and Gongylonema pulchrum) the variance was significantly larger than the mean for the frequency distributions of the number of helminth individuals (Table 2). This is characteristic of an overdispersed distribution (Bliss and Fisher, 1953). The negative binomial parameter, k, was low (<1.0) in these species, indicating aggregation within the host population and for each of

the four host subpopulations delineated by host sex and seasonal variables (Table 2). However, there were no significant differences in the values of k across these four host subpopulations when compared to the average (expected) value for the entire 48 sample dataset (Table 2). This indicated that the degree of overdispersion was homogeneous across the four host subpopulations delineated by host sex and seasons.

Mean abundances of the four species of helminths across the four categories delineated by host sex and seasons are listed in Table 3. Abundances of some species were higher in certain host subpopulations than in others, such as S. dentatus in female swine during the cool season. However, results of the MANOVA and factorial ANOVA (Table 4) indicated that rank abundances of the four common species of helminths collectively and individually did not vary significantly between the main or interactive variables of host sex and/or seasons.

DISCUSSION

At least 30 species of helminths have been reported from feral swine in the southeastern United States (Smith, 1981). Smith et al. (1982) found 22 species of helminths in feral swine from 20 regions in 11 states of the southeastern United

TABLE 2. Determination of overdispersion and measure of degree of aggregation (k) in four common species of helminths from the 48 sample dataset of an insular population of feral swine from Cumberland Island, Georgia.

Species of helminth	Total	Season				Heterogeneity	
		Warm		Cool		Total χ^2	P
		Male	Female	Male	Female		
Stephanurus dentatus	0.413·*	0.512*	0.724*	0.527*	0.227*	2.48	>0.05
Metastrongylus apri	0.577*	0.750*	0.386*	0.383*	0.856*	0.86	>0.05
Metastrongylus pudendotectus	0.119*	0.243*	0.400*	0.667*	0.164*	3.33	>0.05
Gongylonema pulchrum	0.655*	1.137*	0.633*	0.792*	0.351*	0.53	>0.05
Host sample size	48	8	10	12	18		

· Values of k as an inverse measure of overdispersion.
* Variance significantly larger than mean as determined by chi-square analysis of frequency distribution.

States. These included 12 species from five (one adult and four juveniles) feral swine collected on Cumberland Island. All these species of helminths had prevalences ≥20%; six had prevalences ≥40% (Smith, 1981). These feral swine were collected between January 1979 and November 1980. We recovered only nine species of helminths from 48 adult feral swine collected on Cumberland Island between October 1984 and June 1986. Only four species of helminths had prevalences >20%; three had prevalences >40%. All the species we found were recovered also by Smith (1981). We did not recover *Macracanthorhynchus hirudinaceus*, *Oesophagostomum dentatum* or *Strongyloides ransomi* that were found at prevalences of 20, 20 and 60%, respectively, by Smith (1981). Also, there appeared to be a considerable decline in abundances of certain species, including *Ascaris suum*,

Ascarops strongylina, *Globocephalus urosubulatus* and *Oesophagostomum quadrispinulatum*. Conversely, the abundances of *M. apri*, *M. pudendotectus* (regarded as *Metastrongylus* spp. of Smith, 1981), *S. dentatus* and *Physocephalus sexulatus* were greater than reported by Smith (1981). Results of comparisons of data between different studies, especially abundance data across different host age strata with radically different sample sizes (n = 5 versus n = 48), should be interpreted with caution. However, certain apparent trends in prevalence data and the absence of some species from our subsequent collections with a larger sample size necessitate some speculation.

In the early 1970's the feral swine population was "very abundant" on Cumberland Island (Hillestad et al., 1975). During the late 1970's at least 1,200 feral swine were removed by live-trapping (K.

TABLE 3. Average abundances of four common species of helminths across four major category variables delineated by host sex and seasons from the 48 sample dataset of adult feral swine from Cumberland Island, Georgia.

Species of helminth	Season			
	Cool		Warm	
	Male (n = 12)	Female (n = 18)	Male (n = 8)	Female (n = 10)
Stephanurus dentatus	6.3 ± 2.7·	19.4 ± 8.2	8.9 ± 3.1	9.6 ± 6.2
Metastrongylus apri	22.6 ± 7.7	14.5 ± 8.4	18.1 ± 7.2	19.3 ± 6.4
Metastrongylus pudendotectus	4.7 ± 2.8	1.6 ± 1.0	1.0 ± 0.4	7.5 ± 5.6
Gongylonema pulchrum	7.6 ± 2.2	3.3 ± 1.6	5.2 ± 1.5	5.4 ± 2.9

· Mean ± standard error.

TABLE 4. F values generated by MANOVA and factorial ANOVA for main and interactive effects of host sex and season factors across the 48 sample dataset of rank abundances for the four common species of helminths from feral swine on Cumberland Island, Georgia.

	Sex	Season	Sex × season
MANOVA			
Collective helminth species	0.52*	0.36*	0.73*
Factorial ANOVA			
Stephanurus dentatus	1.33*	0.15*	1.91*
Metastrongylus apri	0.05*	0.14*	1.72*
Metastrongylus pudendotectus	0.33*	0.09*	0.05*
Gongylonema pulchrum	0.23*	1.44*	0.05*

* $P > 0.05$.

O. Morgan, pers. comm.). An additional 250 to 350 feral swine were removed from the island by live-trapping and shooting (regulated hunting and scientific collections) from 1980 to 1986 (K. O. Morgan, pers. comm.). The 1979–1980 collections of Smith (1981) were just after the initial herd reduction of feral swine on Cumberland Island. Our collections during 1984–1986 occurred after a relatively longer period (6–8 yr) following reduction of the feral swine and during which time additional individuals were being removed, negating the subsequent effect of yearly juvenile recruitment. The reduced feral swine population could explain the apparent loss of certain helminths which occur at low prevalences such as *M. hirudinaceus* and direct life cycle species such as *O. dentatus* and *S. ransomi* that probably require a certain host population density in order to maintain their transmission potentials. Also, this may be the reason for the overall decline in prevalence of most other helminth species. Alternatively, the absence of certain species such as *S. ransomi* and/or lower prevalences and abundances of species such as *A. suum* may be reflective of host age in our collections versus those of Smith (1981). Four of the five feral swine necropsied and examined for helminths by Smith (1981) were <8 mo of age, while all the animals we examined were >1 yr old. *Strongyloides ransomi* is almost always an infection of young pigs and the abundances of *A. suum* are much

lower in adult than young swine (Levine, 1980).

If the small sample size ($n = 5$) of the 1979–1980 collections (Smith, 1981) provides a reliable estimate, three species of helminths (*M. apri*, *M. pudendotectus* and *S. dentatus*) subsequently appeared to have increased markedly in both prevalence and abundance as reflected in our 1984–1986 collections versus those of Smith (1981). Interestingly, all three species utilize earthworms as intermediate (*Metastrongylus* spp.) or paratenic (*S. dentatus*) hosts and infective larvae can survive for >1 mo in these invertebrates (Levine, 1980). It is tempting to speculate that herd dynamics resulting from recent declines in the population have altered foraging patterns. Also, there was an almost complete mast failure in the fall of 1983 prior to our collections that resulted in increased feral swine rootings for alternative food sources including earthworms (K. O. Morgan, pers. comm.) such that potential exposure to these nematode species was enhanced.

Prestwood et al. (1975) found that only one of 39 possible species of helminths was shared in a similar insular population of feral swine intermingled with white-tailed deer and feral cattle on Ossabaw Island, Georgia. Of the 13 species of helminths in that feral swine population, only *G. pulchrum* was recovered also from the other hosts. The remaining 12 species of helminths were specific to feral swine. *Gongylonema pulchrum* has little or no spec-

ificity and is common in a variety of hosts including white-tailed deer and cattle in the southeastern United States (Prestwood et al., 1970, 1975). This probably accounts for the stability of G. pulchrum in the reduced feral swine population on Cumberland Island. Gongylonema pulchrum was the only species of helminth that appeared to have neither a significant increase nor decrease in prevalence or abundance between the 1979–1980 collections (Smith, 1981) and our 1984–1986 collections.

Anderson (1982) proposed that while demographic and environmental influences act to generate overdispersion in species of parasites, the main factor in natural communities was thought to be heterogeneity in the host populations in the rate at which the parasites establish, survive and reproduce, and that the pattern of distribution seemed to change across seasons and in different host strata. Pence and Windberg (1984) and Corn et al. (1985) purported to substantiate this with examples from helminth communities of coyotes (Canis latrans) and collared peccaries (Dicotyles tajacu), respectively. Wallace and Pence (1986) emphasized that while the relative magnitude of numbers of individuals (abundances) of helminth species may vary dramatically across different host strata (ages, sexes, states of physiological condition, etc.) operating over different seasons, the distribution patterns of most species of helminths are relatively unaffected by these more easily measured extrinsic and intrinsic variables. Thus, it appears that individual host factors (genetic, immunologic, behavioral, etc.) may contribute substantially to the stability of the pattern of overdispersion observed in many species of helminths. In the present study, as in that of Wallace and Pence (1986), the degree of overdispersion was remarkably consistent between heterogeneous host subpopulations across different seasons. This further substantiates the concept that aggregation of helminth individuals within certain host individuals probably constitutes an important element in overdis-

persion that cannot be explained by the more easily measured environmental and intrinsic (host) factors acting on the parasite populations.

Unlike many recent studies (Pence and Windberg, 1984; Corn et al., 1985; Waid et al., 1985; Wallace and Pence, 1986) that have documented significant changes in abundances of species of helminths across different host strata and over seasons, the relative magnitude of the number of individuals of the four common species of helminths in feral swine on Cumberland Island did not vary significantly over the host variable of sex or between warm and cool seasons. Certain species of helminths of domestic swine such as A. suum and S. dentatus are known to occur in greater abundances in young pigs (Levine, 1980). Unfortunately, we examined only adult feral swine from this population. Additionally, Forrester et al. (1982) found significant differences in intensities of three species of lungworms (Metastrongylus salmi, M. apri and M. pudendotectus) across host sexes, host ages, and seasons in feral swine from Florida. We observed no such variations in abundances of two of these species of lungworms (M. apri and M. pudendotectus) from feral swine on Cumberland Island. Whether the present low population density of feral swine on the island has signficantly influenced the pattern of fluctuations in abundances of species of helminths remains to be resolved. Regardless of the reason, this emphasizes that the effects of host and environmental variables on the magnitude of number of individuals in the helminth communities of a particular species of host may vary across different geographical localities, and possibly within the same spatial resource, but in accordance with host population densities.

Because of the specificity of eight of the nine common helminth species in this population of feral swine, it can be assumed that these species were established with the original or later introductions of domestic stock that subsequently became free-rang-

ing. The implications of parasitism on this population of feral swine are difficult to assess. While a number of these species of helminths are pathogenic to pigs reared and maintained under domestic conditions (Levine, 1980), we saw no evidence in the present sample of 48 feral swine from Cumberland Island that helminths were responsible for morbidity or mortality. However, the effect of helminth parasitism on young pigs in this population needs further investigation.

ACKNOWLEDGMENTS

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