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EFFECTS OF HOST AND SPATIAL FACTORS ON A HAEMOPROTEID COMMUNITY IN MOURNING DOVES FROM WESTERN TEXAS

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ABSTRACT: Two species of hematozoa, *Haemoproteus columbae* and *H. sacharovi*, were observed on thin blood smears from populations of mourning doves (*Zenaida macroura*) in the Rolling Plains (RP, a semiarid dryland farming and grazing area) and Southern High Plains (SHP, an intensively cultivated and irrigated agricultural region with playa lakes) of western Texas (USA). Prevalences of *H. columbae* and *H. sacharovi* were 91 and 18% in doves from the RP ($n = 44$ doves examined) and 81 and 36% in those from the SHP ($n = 84$), respectively. Although the prevalences of these species were not significantly different between the RP and SHP, the prevalence of *H. sacharovi* was significantly greater in juvenile versus adult doves from both localities. Mixed infections of both haemoproteid species occurred in 11 and 24% of the doves from the RP and SHP, respectively. The frequency distributions of the relative density values (numbers of parasites/2,000 erythrocytes counted) of *H. columbae* and *H. sacharovi* were overdispersed in hosts from both localities. Relative densities of *H. columbae* were significantly higher in mourning doves from the RP versus the SHP; likewise those of *H. sacharovi* were significantly greater in juvenile versus adult doves and between localities. Observed differences in prevalence and relative density of the two species in the haemoproteid community across spatial and host variables may reflect differences in vector transmission and in the physiological and immunological status of the host. This study emphasizes the importance of using adequately quantified density data versus only prevalence data when examining microparasite communities at the component community level.

Key words: Hematozoa, *Haemoproteus columbae*, *Haemoproteus sacharovi*, mourning dove, *Zenaida macroura*, component level community ecology, host sex effects, host age effects, locality effects, prevalence, relative density, field study.

INTRODUCTION

Most contemporary ecology studies at the component community level on macroparasite (helminths and arthropods) assemblages occupying niches in vertebrate hosts are based on relative density data. Alternatively, because of difficulties associated with quantification, most studies on communities of microparasites, including the parasitic protozoa, have been based on prevalence data. However, even studies utilizing only data on prevalence have indicated trends of changing patterns across host, temporal and spatial variables in communities of such groups as avian haemosporidians (see Greiner, 1970, 1975).

Although there have been attempts to quantify microparasites within host individuals and to examine these data across host and temporal variables, the methods were often subjective (Godfrey et al., 1987). Thus, previous studies on the ecology of

microparasites, such as the avian hematozoa, have been based on only frequency data or, at best, frequency data and subjectively ranked density data. Therefore, these analyses lack the robustness of studies on the community ecology at the component community level of free-living or macroparasitic species where relative distributions in numbers of individuals across a habitat can be considered. Utilizing the methods of Godfrey et al. (1987), we analyzed certain aspects of the component level structure and pattern in a microparasite community using quantified density data. Our objectives were to examine the main and interactive effects of selected host and spatial variables on the hematozoan community in an avian host. We examined the effects of (1) host age, (2) host sex and (3) locality on the prevalence and density of a community of two species of *Haemoproteus* in the mourning dove (*Zenaida macroura*) from western Texas (USA).

MATERIALS AND METHODS

Study area

Doves were collected from localities in Castro County (34°25'N, 102°02'W) and Foard County (33°71'N, 99°38'W) in western Texas. These counties are in the Southern High Plains (SHP) and Rolling Plains (RP) vegetation zones, respectively.

The SHP was originally a short grass prairie which is now used largely for intensive agricultural cultivation of row crops such as corn, grain sorghum and cotton; there are numerous (>0.5 km²) shallow intermittently flooded basins called playas that provide most of the habitat for wildlife in the region (Guthery, 1981; Simpson et al., 1981). Bruns (1974) and Bolen and Guthery (1982) further discuss the characteristics of Castro County.

Major land use features of the RP include dryland grain production and rangeland for cattle. Vegetation in the RP consists of mixed grass species interspersed by juniper (*Juniperus* sp.) breaks and mesquite (*Prosopis glandulosa*) flats. The area is described in detail by Koos and Dixon (1964). The greater availability of wildlife habitat in the RP suggests a more homogeneous distribution of doves than occurs in the SHP where they are concentrated near the playas. Additionally, surveys by the Texas Department of Parks and Wildlife (Austin, Texas 78744, USA) indicate that breeding populations of mourning doves were higher in the RP than the SHP (George, 1988).

Data collection

Mourning doves ($n = 128$) were collected by shooting from 1 to 8 September 1985. We regarded these birds as residents because (1) band recovery analyses of mourning doves harvested in the northern hunting zone of Texas showed that the majority of all birds shot originated from the same zone (Dunks, 1977) and (2) all doves were collected prior to any major cold frontal activity, thus assuring that mainly resident and not northern migrants were collected. Birds were aged by plumage and gonad characteristics (Cannell, 1984; Bivings and Silvy, 1980) and sexed by gonad examination.

Two thin blood smears from each dove were made from heart blood immediately (<1 min) after the bird was collected. Smears were fixed in 100% methanol for 1 min and stained 10 min in phosphate-buffered Giemsa's stain (pH 7.2). This was the same series of blood smears from which representative samples were drawn to develop the quantification methods outlined in Godfrey et al. (1987). Each slide was scanned for 20 min at 1,000 \times magnification to deter-

mine the prevalence of hematozoans. Thus, a total of 40 min was expended to examine both slides from each bird. This period of time allowed scanning of 500 to 700 fields of view. If hematozoans were present, the best slide was selected (based on smear thickness and staining) and 2,000 erythrocytes were counted and examined in 20 replicates of 100 erythrocytes each. The number of each species of *Haemoproteus* was counted and recorded as described by Godfrey et al. (1987). A random-number table was used to determine the number of fields of view to be skipped between each field of view examined. If the field of view was inadequate for examination (viz.—too thick) the observer advanced to the next field of view that was suitable. A field of view was defined as the area circumscribed by the large square of a Miller optical disc (A. O. K1282, American Optical Corporation, Buffalo, New York 14240, USA). All blood smears were examined and hematozoans identified and counted using the same microscope (A. O. Microstar, American Optical Corporation) by the same observer (RDG).

Parasite identification

Prior to quantifying hematozoans in the 128 host individuals, blood smears were scanned as described above to determine prevalence and the representative species were identified following the descriptions of Levine (1973) and Bennett and Peirce (1990). Two species were recognized: *Haemoproteus columbae* and *Haemoproteus sacharovi*. Other species of hematozoans were not seen. Our identifications were confirmed by G. F. Bennett (International Centre for Avian Haematozoa, Memorial University of Newfoundland, St. John's, Newfoundland, Canada A1C 5S7). Representative specimens of these species are deposited in the U.S. National Parasite Collection, USDA ARS, Building 1180 BARC-East, Beltsville, Maryland 20705, USA; accession numbers 79666 and 80560 and the International Centre for Avian Haematozoa (accession number 97895a,b).

Definitions

The terms prevalence and abundance (relative density) follow the definitions of Margolis et al. (1982). Density is used in terms of the number of infected erythrocytes/total number of erythrocytes counted in a particular host individual. Use of the terms component community level and infracommunity is in accordance with the definitions of Holmes and Price (1986). Throughout the text usage of the terms significant and significantly refer to statistical significance.

Data analyses

Categorical data modeling (PROC CATMOD; Statistical Analysis Systems, 5th Edition, SAS Institute, Inc., Cary, North Carolina 27511, USA) on frequency data was used in a factorial design to determine, by chi square analysis, the main and interactive effects of host age, host sex and locality on prevalences of haemosporidians. Statistical methods for determining the number of erythrocytes that needed to be counted in each blood smear to provide a realistic estimate of the density and for determining if the sample population densities met the assumptions for a normal distribution were those of Godfrey et al. (1987). Because the frequency distributions of relative density values were overdispersed and the distribution of residual errors did not meet the assumptions for a normal distribution, the rank transformation procedure of Conover and Iman (1981) was applied to this data set prior to further analysis (PROC RANK; SAS). A value of $N = 1$ was added to each density value for all infected birds in order to include data from those birds in which the density could not be quantified ($N = <1$ parasite/2,000 erythrocytes). Factorial ANOVA (PROC GLM; SAS) for the individual parasite species and MANOVA (PROC GLM; SAS) for both parasite species collectively determined the main and interactive effects of the independent variables of host age, host sex and locality on the ranked densities of the dependent variables of *H. columbae* and *H. sacharovi*. Statistical significance was determined at the level of $P \leq 0.05$.

RESULTS

Data on prevalences of *Haemoproteus* spp. in mourning doves from two localities in western Texas are presented in Table 1. Prevalence of doves infected with one or both species of *Haemoproteus* from the RP was 98% compared to 93% of the doves from the SHP. The prevalence of *H. columbae* was higher in the RP (91%) than in the SHP (81%). For *H. sacharovi* the prevalence was higher in the SHP (36%) than in the RP (18%). Prevalence of *H. sacharovi* was lower in adults (22%) than juveniles (35%). Prevalence of mixed infections of *H. columbae* and *H. sacharovi* was always lower than the prevalences for individual species (Table 1). Despite these apparent differences, Categorical Data Modeling indicated no statistically significant differences in prevalence across any

of the main or interactive effects of host age, host sex or locality (Table 2).

The mean densities of *H. columbae* were higher in the RP versus the SHP across all subpopulations of hosts. Also, the densities were higher in juvenile versus adult doves in both areas except for female adults in the SHP. Secondly, the densities of *H. sacharovi* were much higher in juvenile versus adult doves in both localities.

Analyses of density data for haemoproteids of mourning doves indicated significant differences across host and locality variables which were not detected using prevalence data. With the factorial ANOVA for ranked densities of individual species and MANOVA for both species collectively across the independent variables of host age, host sex and locality the apparent differences in haemoproteid densities (Table 3) were significant as main effects for (1) locality with *H. columbae* and *H. sacharovi*, and (2) age with *H. sacharovi* (Table 4). Significant interactive effects of locality-age resulted from the higher densities of *H. columbae* in juvenile versus adult doves in the SHP except for the female adults in the RP which had much higher densities than all other subpopulations in both localities. The latter accounted for a significant locality-sex interactive effect.

DISCUSSION

The prevalence of single and mixed infections of *H. columbae* and *H. sacharovi* in mourning doves from western Texas were similar to those reported in white-winged doves (*Zenaida asiatica*), from the lower Rio Grande Valley of Texas (Stabler, 1961). However, these prevalences were somewhat higher than those reported in mourning doves from adjacent localities including north central Texas (Couch, 1952), western Oklahoma (Lewis et al., 1975), Nebraska (Greiner, 1975), central New Mexico (Gutierrez, 1973), and Colorado (Stabler and Holt, 1963). The higher prevalences and significant differences in densities of *H. sacharovi* that we observed

TABLE 1. Prevalence of *Haemoproteus* spp. in mourning doves from western Texas.

	Locality					
	Rolling Plains			Southern High Plains		
	<i>H. columbae</i>	<i>H. sacharovi</i>	Both	<i>H. columbae</i>	<i>H. sacharovi</i>	Both
Adult male	90 ^a 9/10 ^b	0 0/10	0 0/10	93 13/14	21 3/14	14 2/14
Juvenile male	94 15/16	25 4/16	19 3/16	67 18/27	37 10/27	19 5/27
Adult female	100 5/5	20 1/5	20 1/5	90 19/21	33 7/21	24 5/21
Juvenile female	85 11/13	23 3/13	8 1/13	82 18/22	45 10/22	36 8/22
Total	91 40/44	18 8/44	11 5/44	81 68/84	36 30/84	24 20/84

^a Percent.

^b Number infected/number examined.

agree with the results of Hanson et al. (1957) but contrasted with those of Greiner (1975) who found higher prevalences of this parasite in adult than juvenile mourning doves.

The higher prevalences and significantly higher densities of *H. columbae* in the RP versus the SHP may be reflective of biogeographical differences between these localities as related to both distribution and habitat preferences of the vector(s). However, there is no information on which vector(s) is(are) utilized by these haemoproteids from mourning doves or on the biology of hippoboscids or other potential vectors such as *Culicoides* spp. (Greiner, 1975) in western Texas.

Our results indicating higher prevalences and significantly higher densities of

H. sacharovi in juvenile versus adult doves could be explained in terms of the changing immunological and physiological status of the host. Relapses of these and other species of *Haemoproteus* are discussed by Coatney (1933) and Farmer (1962). During the host's life cycle and also possibly in response to temporal (seasonal) changes, intensities of gametocytes in peripheral circulation vary; during the prepatent and latent periods the pre-erythrocytic schizonts occur in the host tissues, and gametocytes disappear from peripheral circulation. Thus, our estimates of values for prevalence and, to a lesser extent, density in adult doves may be underestimated (i.e., latent infections).

The hematozoan community consisting of two species of *Haemoproteus* infecting

TABLE 2. ANOVA table from categorical data modeling analysis showing results of factorial ANOVA of chi square values from frequency data of two *Haemoproteus* spp. in the 128-sample data set across two locality, host age and host sex classes of mourning doves from western Texas.

Effect	<i>H. columbae</i>		<i>H. sacharovi</i>		Both	
	F	P	F	P	F	P
Locality	0.51	0.475	3.11	0.078	2.95	0.400
Age	1.04	0.309	2.21	0.137	1.51	0.680
Sex	0.02	0.880	1.19	0.270	0.86	0.836
Locality-age	0.91	0.341	0.13	0.723	2.50	0.475
Locality-sex	0.28	0.600	0.06	0.808	0.65	0.885
Age-sex	0.00	0.995	0.76	0.382	0.96	0.811
Locality-age-sex	0.71	0.401	0.42	0.519	1.27	0.735

TABLE 3. Mean densities of *Haemoproteus* spp. from mourning doves in western Texas.

Host	Locality			
	Rolling Plains		Southern High Plains	
	<i>H. columbae</i> $\bar{x} \pm SE$	<i>H. sacharovi</i> $\bar{x} \pm SE$	<i>H. columbae</i> $\bar{x} \pm SE$	<i>H. sacharovi</i> $\bar{x} \pm SE$
Adult male	15.3 \pm 7.4 ^a	0 ^b	3.5 \pm 1.2	1.7 \pm 1.7
Juvenile male	24.1 \pm 7.4	20.8 \pm 19.4	6.7 \pm 2.4	9.4 \pm 5.1
Adult female	1.8 \pm 0.4	0 ^c	16.8 \pm 6.5	0.7 \pm 0.4
Juvenile female	12.5 \pm 2.9	24.7 \pm 12.4	8.8 \pm 2.5	3.7 \pm 1.7

^a Number of parasites/2,000 erythrocytes.

^b No parasites.

^c <1 parasite/2,000 erythrocytes.

erythrocytes of resident mourning doves from two localities in western Texas provided a simplistic model for examining the component level community structure of this guild of blood-dwelling protozoans. Our study illustrates the importance of using both prevalence and quantified density data when examining differences in patterns and structure in these parasite communities at the component community level across different host and spatial variables. Prevalence data expresses the actual frequency of occurrence of the respective parasite species in the host population. Density (abundance) data not only express their presence or absence, but is reflective of the number of individuals for each parasite species at the infracommunity level; it can be summarized (mean densities) across biotic, spatial and temporal variables at the component community level.

TABLE 4. Values of the F statistic generated from factorial ANOVA for each species and MANOVA for both species collectively on densities of *Haemoproteus* spp. from mourning doves across variables of locality, host age and host sex.

Variable	<i>H. columbae</i>	<i>H. sacharovi</i>	Total
Locality	7.61 ^a	4.78 ^a	5.56 ^a
Age	1.21	6.09 ^a	3.96 ^a
Sex	0.22	0.20	0.19
Locality-age	5.68 ^a	0.18	3.05 ^a
Locality-sex	8.39 ^a	0.12	4.38 ^a
Age-sex	0.06	0.00	0.03
Locality-age-sex	0.26	0.02	0.15

^a Significant at $P \leq 0.05$.

While prevalences may remain equivalent with no significant differences, densities may vary across these variables indicating trends that would remain otherwise undetected. Such was the case in this study on the haemoproteid community from mourning doves.

Unfortunately, the presence of only two species in the community of hematozoa from mourning doves precluded any meaningful comparisons of diversity across localities and/or host subpopulations. Likewise, in most studies at the component community level involving macroparasite communities, temporal (seasonal) factors appear to be as significant an influence as host age in determining changes in parasite densities (see Pence, 1990). Unfortunately, our single fall collections precluded evaluation of the temporal aspects as a factor in the changing dynamics of the community of parasites of these populations of mourning doves. However, in the factors that were examined the pattern and structure of this haemoproteid community seemed to follow many of the same trends that often occur in helminth communities, especially across host subpopulations differentiated by age and different geographic localities (Pence, 1990). Our study emphasizes that while analysis of prevalence data may indicate certain broad trends, examination of density (abundance) data may indicate even greater variation across host, spatial and temporal variables acting on these parasite populations. We believe

that these kinds of analyses can contribute important new information on the epidemiology of blood dwelling protozoa and, especially, they can provide the focal points for initiation of additional research.

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