

HELMINTH COMMUNITY STRUCTURE IN AN EXPANDING WHITE-WINGED DOVE (*ZENAIDA ASIATICA ASIATICA*) POPULATION

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ABSTRACT: Helminth communities of 171 fledged white-winged doves (*Zenaida asiatica asiatica*) from the expanding eastern population in Texas (USA) were examined from hosts collected 11 June to 19 September 1997 within their historical range, new breeding periphery, and an intermediate area. Eleven helminth species, representing 435 individuals, were found. Helminths occurred in three microhabitats, of which the small intestine was the most commonly occupied. Nematodes dominated numerically (76% of total worms), followed by cestodes (17%), and trematodes (7%). Infracommunities were species-poor; the most complex infracommunity consisted of three helminth species, which occurred in three host individuals, followed by two species that occurred in 13 hosts. The remaining 155 doves had one (70) or no (85) species. The overall helminth component community was species-poor and was dominated by *Ascaridia columbae* which occurred in 26% of the white-winged doves and accounted for 65% of all helminth individuals. Prevalence and abundance of *A. columbae* varied by geographic region and host age, but not by host sex. Helminth component communities varied by geographic region, host age, and host sex. These differences were primarily attributable to unique occurrences of uncommon species within specific host subpopulations. Results suggest that the white-winged doves' multimodal regional abundance pattern, sympatry with other columbids, and granivorous diet may be more important in shaping helminth community structure than the influences often associated with geographic range expansion.

Key words: Community ecology, component communities, helminths, Texas, white-winged doves, *Zenaida asiatica*.

INTRODUCTION

Community ecologists are often interested in determining if communities show predictable structure and, if they do, determining the underlying processes (Holmes, 1986; Gaston et al., 1997). Examination of certain helminth communities suggests structure, which has spurred interest in applying and refining various ecological hypotheses to describe the nature of these communities (Holmes and Price, 1986; Esch et al., 1990).

Within the context of assessing influences on helminth community structure, interest has been focused on host geographic distribution patterns (Gregory, 1990; Kennedy and Bush, 1994; Poulin, 1999; Poulin and Morand, 1999). Several parasite studies conducted on expanding host populations have found that helminth assemblages at the periphery of the host's range are depauperate and comprised largely of un-

common species (Fedynich et al., 1986; Radomski et al., 1991). These studies suggested that helminth communities reflected characteristics of Brown's (1984) resource breadth hypothesis, in which abundance of a species is greatest near the core of its geographic range where the most favorable conditions occur and declines gradually to zero at the boundaries of its range. Because hosts represent helminth habitats, helminth community structure should reflect host abundance across the host's geographic range (Radomski et al., 1991).

Eastern white-winged doves (*Zenaida asiatica asiatica*) afford an opportunity to examine the helminth community of an expanding host population that does not experience extreme migration patterns. Historically, the breeding population of eastern white-winged doves occurred in the Lower Rio Grande Valley (LRGV) of Texas

and adjoining Mexican state of Tamaulipas (George et al., 1994). During the last 40 yr, a significant northward range expansion occurred into central, north, and east Texas (George et al., 1994). Presently, pioneering breeding colonies of eastern white-winged doves are extending into northern and northeastern Texas. The extent of this range expansion became evident in 1990, when more white-winged doves were estimated to breed north of the LRGV than in the LRGV (West et al., 1993). However, these birds are almost exclusively found in urban habitats, compared to those occurring in the LRGV, which occupy urban, citrus grove, and brushland habitats (Small and Waggener, 1999). Many urban areas provide the necessary habitat for winter survival, which has resulted in a substantial number of eastern white-winged doves overwintering in Texas (George et al., 1994) despite the relatively short distance to traditional wintering areas in Central America (George et al., 2000). Because urban habitats permit white-winged doves to extend their breeding season up to 75% beyond those that nest in the LRGV (Hayslette and Hayslette, 1999), young that are hatched late in the season probably are not mature enough to undergo migration, which further contributes to the number of overwintering white-winged doves in Texas.

The present study was initiated to assess the helminth community in an expanding granivorous host population. Our objectives were to: (1) determine helminth infra- and component communities in the eastern population of white-winged doves in Texas; (2) compare and contrast helminth community structure and pattern in white-winged doves from the historical breeding area and northern breeding periphery in Texas; (3) determine the influence of host age and sex on the helminth community; and (4) relate these findings to host-parasite interactions.

MATERIALS AND METHODS

Study area

White-winged doves were collected from three geographic regions: (1) LRGV, represent-

ing the original breeding range of eastern white-winged doves in Texas (Starr, Hidalgo, Cameron, and Willacy counties; 25°59'N to 26°18'N, 97°32'W to 98°39'W); (2) the new breeding periphery, located in northern and eastern Texas (Tom Green, Taylor, Brown, McLennan, Bell, and Galveston counties; 31°05'N to 32°23'N, 97°08'W to 100°29'W); and (3) central Texas, an intermediate area (Uvalde, Bexar, Bee, and Wilson counties; 28°28'N to 29°34'N, 97°43'W to 99°45'W). Linear distance from areas sampled in the LRGV to the areas at the breeding periphery was approximately 450 km.

Host data collection

We collected 171 fledged juvenile and adult white-winged doves by shooting from 11 June to 19 September 1997. Fifty-seven (17 juveniles, 40 adults), 60 (32 juveniles, 28 adults), and 54 (26 juveniles, 28 adults) birds were collected from the LRGV, central Texas, and the breeding periphery, respectively.

White-winged doves were eviscerated within 10 min of death. Viscera from each dove was placed in individually marked plastic bags and frozen using a mixture of ethyl alcohol and dry ice. Carcasses were placed in individually marked plastic bags. Both carcasses and viscera were placed in coolers containing wet and/or dry ice, transported from the field, and stored in a laboratory freezer at -10 C. White-winged doves were collected in accordance with established guidelines and protocols of Texas Parks and Wildlife Scientific Collection Permit Nos. SPR-0496-773, SPR-0497-877, and SPR-0697-897 (Austin, Texas) and U.S. Fish and Wildlife Service Permit Nos. PRT-800477 and PRT-829139 (Albuquerque, New Mexico).

Helminth data collection

Carcasses and viscera were examined for helminths according to procedures outlined in Fedynich (1993). Microhabitats examined included: eye surface and nictitating membrane, nasal cavity, nasal sinus, suborbital sinus, brain, trachea, syrinx, lung, heart, kidney, liver, esophagus, proventriculus, gizzard, pancreas, spleen, small intestine, large intestine, cloaca, reproductive tract, and body cavity.

Nematodes were fixed in glacial acetic acid, stored in a mixture of 70% alcohol and 8% glycerin, and examined with a microscope and/or dissection scope in alcohol-glycerin wet mounts. Trematodes and cestodes were fixed in acid-formalin-ethyl alcohol (AFA) solution, stored in 70% alcohol, and examined in alcohol wet mounts. If necessary for identification, nematodes were cleared in glycerin and trem-

atodes and cestodes were stained with Semichon's acetocarmine.

Helminth specimens were identified following taxonomic keys of Schell (1970), Schmidt (1986), Skrjabin (1961), Sonin (1974), and Wardle and McLeod (1968). *Ornithostrongylus minutus* (possibly a synonym of *O. quadriradiatus*) was identified following Travassos (1940). Male *O. minutus* and *Oswaldostongylus* spp. were readily recognizable, but females could not be differentiated. Consequently, *O. minutus* and *Oswaldostongylus* spp. were combined and referred to as the Strongloidea complex. *Brachylaima mazzanti* and *Philopthalmus gralli* were identified by J. M. Kinsella (Department of Pathobiology, College of Veterinary Medicine, University of Florida, Gainesville, Florida, USA). Our identifications of the remaining helminths were confirmed by D. B. Pence (Department of Pathology, Texas Tech University Health Sciences Center, Lubbock, Texas, USA). Representative specimens of helminth species were deposited in the U.S. National Parasite Collection (Beltsville, Maryland 20705, USA; USNPC Nos. 090175–090180).

Definitions

The terms prevalence, intensity, mean intensity, and abundance follow the definitions of Bush et al. (1997). Common helminth species were defined as those with $\geq 70\%$ prevalence across the collective host sample, intermediate species $\geq 20\%$ and $< 70\%$, and rare or uncommon species $< 20\%$. Infracommunity refers to all infrapopulations of parasite species occurring within a single host and component community refers to all infrapopulations of parasites occurring within a particular subset of a host species (Bush et al., 1997). The term microhabitat refers to anatomical localities within the host.

Parasite analyses

Frequency data for species with $\geq 20\%$ prevalence across the collective host sample were analyzed with log-linear models (CATMOD; SAS Institute, Inc., 1990). This method was used to determine if prevalence varied by the main effects of geographic region (historical, intermediate area, breeding periphery), host age (juvenile, adult), and host sex (male, female).

The frequency distribution pattern of abundance for species with $\geq 20\%$ prevalence across the collective host sample was tested for normality (PROC UNIVARIATE NORMAL; SAS Institute, Inc., 1990). Because a non-normal distribution pattern (aggregation) occurred,

abundance values were rank-transformed (PROC RANK; SAS Institute, Inc., 1990) prior to further statistical analyses. Rank-transformed abundance values were examined for the main (region, age, and sex) and interactive (region \times age, region \times sex, and age \times sex) effects with analysis of variance (ANOVA; SAS Institute, Inc., 1990) in which significant means were separated using least squares means procedure (LSM; SAS Institute, Inc., 1990).

Descriptive statistics are presented as a mean \pm 1 SE. Probability values generated from log-linear models (Chi-square) are presented as exact *P* values; those from ANOVA are presented as the probability (*P*) of a greater *F* value.

The percentage similarity index (PS_i; Pielou, 1975) was used to evaluate numerical similarity of helminth communities between geographic regions, host age, and host sex, based on the relative proportion of helminth individuals contributed by each helminth species. Jaccard's coefficient of similarity index (*J*_i; Krebs, 1989) was used to measure the similarity of shared species between geographic regions, host age, and host sex. Numerical dominance index (*D*_i) of Leong and Holmes (1981) was used to rank helminth species by the number of individuals that each species contributed to the total number of helminth individuals by geographic region, host age, and host sex.

RESULTS

Eleven helminth species (two trematodes, four cestodes, and five nematodes), representing 435 individuals were found in 171 white-winged doves (Table 1). Nematodes dominated numerically (76% of total worms), followed by cestodes (17%) and trematodes (7%). Four helminths, *B. mazzanti*, *P. gralli*, *Sobolevicanthus* sp., and *Splendidofilaria* sp., have not been previously reported in white-winged doves from the United States.

Microhabitats occupied by helminths included the small intestine, proventriculus, and nasal cavity, of which the small intestine was the most commonly occupied. At the infracommunity level, most of the microhabitats were vacant. Three, two, one, and zero helminth species occurred in 3, 13, 70, and 85 white-winged doves, respectively.

Ascaridia columbae was the most prevalent species, which occurred in 26% of the white-winged doves and accounted for

TABLE 1. Descriptive statistics of helminths from 171 white-winged doves collected during summer 1997 in Texas.

Helminth species	Prevalence		Intensity		Abundance	
	Number infected	%	$\bar{x} \pm SE$	Range	$\bar{x} \pm SE$	Total
DIGENEA						
<i>Brachylaima mazzanti</i> (SI) ^a	5	3	5.6 ± 1.6	3–12	0.2 ± 0.1	28
<i>Philothalmus gralli</i> (NC) ^b	1	<1	1.0 ± 0	1	<0.1 ± <0.1	1
CESTODA						
<i>Killigrewia delafondi</i> (SI)	19	11	1.6 ± 0.3	1–5	0.2 ± <0.1	31
<i>Raillentina</i> spp. ^c (SI)	3	2	3.3 ± 0.3	3–4	0.1 ± <0.1	10
<i>Sobolevicanthus</i> sp. (SI)	11	6	3.1 ± 0.8	1–7	0.2 ± 0.1	34
NEMATODA						
<i>Ascaridia columbae</i> (SI)	44	26	6.5 ± 1.1	1–33	1.7 ± 0.4	284
<i>Dispharynx nasuta</i> (PR)	1	<1	1.0 ± 0	1	<0.1 ± <0.1	1
Strongyloidea complex ^d (SI)	20	12	2.3 ± 0.5	1–10	0.3 ± 0.1	45
<i>Splendidofilaria</i> sp. (SI)	1	<1	1.0 ± 0	1	<0.1 ± <0.1	1

^a Microhabitats: SI, small intestine; NC, nasal cavity; PR, proventriculus.

^b Although found in the nasal cavity, microhabitat for *Philothalmus* spp. is generally regarded to be the eye surface and nictitating membrane.

^c Complex of two unidentified species.

^d Complex of at least two species: *Ornithostrongylus minutus* and *Oswaldostrongylus* spp.

65% of all helminth individuals (Table 1). The remaining species rarely occurred ($\leq 12\%$ prevalence) and individually contributed little ($\leq 10\%$ of total worms) to the component community. Prevalence of *A. columbae* varied ($P = 0.0009$) among

TABLE 2. Abundance of *Ascaridia columbae*, least squares means of ranked abundance data, and associated P values generated from ANOVA for the main effects of geographic region, host age, and host sex of 171 white-winged doves collected during summer 1997 in Texas.

Main effect	Abundance	LS means	P
Geographic region			
LRGV ^a	0.2 ± 0.2	66.5 A ^b	0.0001
Intermediate	2.8 ± 0.8	98.3 B	
Periphery	2.0 ± 0.6	92.5 B	
Host age			
Juvenile	0.8 ± 0.4	73.0 A	0.0001
Adult	2.3 ± 0.5	98.4 B	
Host sex			
Male	2.0 ± 0.6	87.3 A	0.57
Female	1.1 ± 0.3	84.2 A	

^a Lower Rio Grande Valley of Texas.

^b Least squares means with same letter within each main effects category are not significantly different.

regions, in which prevalence in hosts collected from the LRGV (5%) was lower than those in the intermediate and peripheral areas (38% and 33%, respectively). Prevalence of *A. columbae* was higher ($P = 0.002$) in adults than juveniles (35% and 14%, respectively); there was no difference ($P = 0.58$) between males and females. Rank abundance of *A. columbae* was lower in doves from the LRGV, compared to those in the intermediate and peripheral areas (Table 2). Rank abundance was higher in adults than in juveniles, but was similar between host sex (Table 2). An interactive effect occurred between host age and geographic region ($P \leq 0.005$), in which adults from the LRGV had lower rank abundance than adults from intermediate or peripheral areas; juveniles from the intermediate area had lower rank abundance than adults from intermediate or peripheral areas, and adults from the intermediate area had higher rank abundances than juveniles or adults from the peripheral area.

Helminth component communities varied across geographic regions (Tables 3, 4).

TABLE 3. Helminth community analyses by geographic region, host age, and host sex using percentage similarity (PS_i) and Jaccard's (J_i) indices for 171 white-winged doves collected during summer 1997 in Texas.

Comparison	PS_i	J_i
LRGV ^a and intermediate area	0.50	0.49
Intermediate area and periphery	0.57	0.69
LRGV and periphery	0.38	0.28
Juvenile and adult	0.67	0.79
Male and female	0.56	0.77

^a Lower Rio Grande Valley of Texas.

The intermediate and peripheral areas were the most similar in helminth community composition, whereas communities found in the LRGV and breeding periphery were the most dissimilar (Table 3). Dominance index values also showed major differences in community structure (Table 4).

There were several unique occurrences of helminth species by geographic region (Table 4). Two species, *P. gralli* and *Splendidofilaria* sp., were found only in the LRGV while three other species were not found in the LRGV. Additionally, *Raillientina* spp. were found only at the breeding periphery.

Helminth community composition was dissimilar between host age groups and

host sex groups (Tables 3, 4). Unique occurrences among host age and host sex were the result of three uncommon species (*P. gralli*, *Dispharynx nasuta*, and *Splendidofilaria* sp.) two of which were found exclusively in adults and one in a juvenile. By sex, one occurred in a male and two occurred in females. These species were unique to these host subclasses because each occurred as a single specimen. Also, there were five occurrences of *B. mazzanti*, found only in females.

DISCUSSION

The helminth component community in white-winged doves from Texas was species poor, contained few helminth individuals, and was comprised largely of rare species. This characterization did not change when examining component communities by geographic region even though differences in PS_i , J_i , and D_i were found between communities occurring at the LRGV and breeding periphery. Our findings suggest other factors are exerting a strong influence on community structure that have been absent in previous studies that have used Brown's (1984) resource breadth hypothesis to describe host-parasite systems at the periphery of a host's range (Fedynich et al., 1986; Radomski et

TABLE 4. Dominance index values generated for helminths by geographic region, host age, host sex, and the collective host sample from white-winged doves collected during summer 1997 in Texas.

Helminth species	Geographic region			Host age		Host sex		Total <i>n</i> = 171
	LRGV ^a <i>n</i> = 57	Int. area ^b <i>n</i> = 60	Periphery <i>n</i> = 54	Juvenile <i>n</i> = 74	Adult <i>n</i> = 97	Male <i>n</i> = 107	Female <i>n</i> = 64	
<i>Ascaridia columbae</i>	15.6	85.1	65.0	53.9	69.4	79.2	42.4	65.3
Strongyloidea complex ^c	50.6	3.1	0	5.2	12.2	6.7	16.4	10.4
<i>Sobolevicanthus</i> sp.	13.0	1.0	13.5	18.2	4.0	4.8	12.7	7.8
<i>Killigrewia delafondi</i>	18.2	7.7	1.3	12.2	5.3	7.4	6.7	7.1
<i>Brachylaima mazzanti</i>	0	2.6	14.1	6.1	6.6	0	17.0	6.5
<i>Raillientina</i> spp. ^d	0	0	6.1	3.5	1.9	1.5	3.6	2.3
<i>Philopthalmus gralli</i>	1.3	0	0	0	0.3	0.4	0	0.2
<i>Dispharynx nasuta</i>	0	0.5	0	0.9	0	0	0.6	0.2
<i>Splendidofilaria</i> sp.	1.3	0	0	0	0.3	0	0.6	0.2

^a Lower Rio Grande Valley of Texas.

^b Intermediate area.

^c Complex of at least two species: *Ornithostrongylus minutus* and *Oswaldostrongylus* spp.

^d Complex of two unidentified species.

al., 1991). Three factors relevant to white-winged doves in our study were their regional abundance pattern, sympatry with phylogenetically-related hosts, and diet.

In the LRGV and northern Mexico, preferred habitats are mainly in rural areas, whereas north of the LRGV, white-winged doves occur in urban areas (George et al., 1994). Urban areas represent habitat patches or islands in which large populations of white-winged doves often occur, even at the breeding periphery. Consequently, the white-winged dove population, exhibits a multimodal abundance pattern resulting from habitat patchiness (i.e., occurrence mainly in urban areas outside of the LRGV). This type of abundance pattern is an exception to Brown's (1984) hypothesis as it represents a violation of the assumption that environmental similarity is a continuously decreasing function of the distance between sites extending towards the range boundary.

At a much smaller spatial scale, local urban populations of white-winged doves commonly exploit bird feeders (George et al., 1994) and backyard waterers. Hosts concentrating at these sites can facilitate helminth transmission, which may explain certain patterns observed in our study. For example, we found helminth communities from the intermediate and peripheral areas tended to be more similar than those from the LRGV. Additionally, abundance of *A. columbae* was substantially lower in the LRGV than in the intermediate and peripheral areas, which suggested higher rates of transmission in urban areas where host densities were higher.

Second, mourning doves (*Zenaida macroura*), Inca doves (*Columbina inca*), ground doves (*Columbina passerina*), and rock doves (*Columba livia*) are regionally sympatric with white-winged doves in Texas, which also are potential hosts. Thus, when viewed at the host family level, range expansion of white-winged doves in Texas is occurring within the core ranges of other columbids. Given the influence of phylogenetically-related host species in shap-

ing helminth communities (Kennedy and Bush, 1994; Poulin, 1997), columbid density and distribution patterns likely have an effect on helminth community structure and pattern in white-winged doves.

Third, host diet is an important component in shaping helminth communities (Goater et al., 1987). Kennedy et al. (1986) suggested hosts that have generalist diets tend to have diverse helminth communities, while hosts that feed selectively tend to have helminth communities that are dominated by large infrapopulations of a few helminth species. In our study, infrapopulations were not particularly large, helminth communities were dominated by either *A. columbae* or the Strongyloidea complex (*O. minutus* and *Oswaldostongylus* spp.), and trematodes and cestodes rarely occurred. These findings support the thesis that a granivorous diet substantially decreases the acquisition of helminths, particularly those with an indirect lifecycle.

The present study emphasizes that helminth communities in the expanding eastern white-winged dove population do not necessarily demonstrate characteristics found in other expanding host populations at the periphery of the host's range. This likely resulted from differences in local host abundance attributable to the regional distribution of habitat patches within the area of range expansion, occurrence of phylogenetically-related host species, and specialization of host diet.

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