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# HELMINTH COMMUNITY COMPOSITION, STRUCTURE, AND PATTERN IN SIX DOVE SPECIES (COLUMBIFORMES: COLUMBIDAE) OF SOUTH TEXAS

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ABSTRACT: The helminth community composition and structure of 6 species of columbids residing in south Texas are reported and compared herein. Sixty individuals of the following species, rock pigeons (*Columba livia* [RP]), mourning doves (*Zenaida macroura* [MD]), Eurasian collared-doves (*Streptopelia decaocto* [ECD]), white-winged doves (*Zenaida asiatica* [WWD]), and common ground doves (*Columbina passerina* [CGD]), and 48 Inca doves (*Columbina inca* [ID]) were collected during the summer of 2006 and examined for helminths. Twelve helminth species were found (9 nematodes and 3 cestodes), representing 486 individuals. Nematodes numerically dominated the component community in all host species. Overall, helminth prevalence was similar among host sex within all dove species. However, prevalence of *Skrjabinia bonini* and *Hymenolepis* sp. in RPs was significantly different among host age groups ($P = 0.01$, $P = 0.0002$, respectively). Likewise, prevalence of *Killigrewia delafondi* was higher ($P = 0.0001$) in adult WWDs. Based on percent similarity and Jaccard's coefficient of community indices, helminth component communities were dissimilar, and the number of shared helminth species varied among host species. Data from this study suggest that the environment surrounding preferred host habitat and foraging strategies of each host species is the driving force behind helminth component communities. This study emphasizes the importance of examining co-occurring hosts at both local and regional scales to elucidate helminth community structure and patterns.

Columbids are versatile; they have near-worldwide distributions, occupy variable geographical ranges, exist in diverse habitat types, and are capable of coexistence with other dove species. Component community studies have often focused on single columbid species (e.g., Glass et al., 2002; Lee et al., 2004), whereas fewer studies have examined the influence of co-occurring host species (Conti and Forrester, 1981; Fedynich et al., 1997; Forrester and Spalding, 2003). Examination of multiple phylogenetically related co-occurring hosts may provide insight into the ways in which host communities influence helminth community structure and patterns.

Two fundamental approaches have been used to evaluate the roles of phylogeny and ecology as determinates of host–parasite associations. The first operates under the assumption of host–parasite specialization as the result of close evolutionary association (Johnson and Clayton, 2004). Here, host and parasite phylogenies should remain in complete congruence, where speciation in the host lineage results in speciation of the parasite lineage (cospeciation), with the opportunity of reduced congruence as the result of ecological factors (Johnson and Clayton, 2004; Brooks et al., 2006). The second examines incongruence in host–parasite phylogenies as the result of processes other than cospeciation, such as ecological, physiological, and/or immunological factors (Brooks, 1979). Brooks et al. (2006) communicates the need to redirect analysis of these associations in terms of "traits rather than taxonomy," such that assemblages might be shaped by the distribution of phylogenetically conserved traits (i.e., "ecological fitting"; Janzen, 1985).

Although hosts utilized in this study are phylogenetically related, a habitat utilization gradient exists (Appendix A) among, and within, species, facilitating assumptions pertaining to host–parasite associations among taxa. If similar helminth species are discovered to parasitize closely related columbid taxa, that will be evidence for cospeciation. However, if helminth assemblages are similar among host species in geographically close/ecologically similar habitats, that will suggest that ecology influences infection patterns (ecological fitting).

Appendix A includes a brief overview outlining the patterns of distribution, habitat range, feeding habits, and foraging behavior for each host species examined. Nested within the host community utilized in this study, there are suites of characteristics unique to previous studies of helminth community composition and structure. First, 2 sets of congeners are presented in this study, i.e., the Inca dove (*Columbina inca* [ID]) and common ground dove (*Columbina passerina* [CGD]), and the mourning dove (*Zenaida macroura* [MD]) and white-winged dove (*Zenaida asiatica* [WWD]), facilitating the comparison of helminth communities along the gradient of relatedness (cospeciation). Second, 4 species are native to the New World (MD, WWD, CGD, and ID), while 2 are exotic, i.e., Eurasian collared-dove (*Streptopelia decaocto* [ECD]) and rock pigeon (*Columba livia* [RP]). Third, within the exotic subset of hosts (RP and ECD), a temporal scale occurs, facilitating time-wise comparisons of helminth community and structure. The RP was introduced into the New World in the early seventeenth century (Johnston, 1992), while the ECD is a more recent introduction (ca. 1972).

## MATERIALS AND METHODS

### Study area

Columbids were collected from Kleberg, Jim Wells, Brooks, and Kenedy Counties in south Texas, better known as the south Texas Coastal Plains. This area is dominated by drought-tolerant shrubs and small trees. Several plant communities are represented in this region, and they have been described in detail by Weakley (2000). Plant communities included in this region are upland grasslands, live oak savannas, upland mesquite savannas, and blackbrush xerophytic brush. The south Texas study area was chosen to facilitate analyses of helminth communities within a community of doves that co-occur regionally. The counties represented by this study area encompass several habitat types that are utilized by all 6 columbid species, including urban (residential), suburban, and rural (semiarid brushlands and agricultural) areas.

### Host collection

Sixty individuals of the following species, RP, MD, ECD, WWD, and CGD, and 48 ID were collected by shotgun, pellet gun, and trapping (urban areas where firearm collection was prohibited) during the summer of 2006 from both nesting/roosting and foraging habitats. An equal

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sample size of adults, juveniles, males, and females was attempted to facilitate analyses. Hosts were aged and sexed in the field prior to shooting utilizing characteristics unique to each host species. Each dove was labeled by host ID number, location, species, gender, and age. Doves were either transported directly to Caesar Kleberg Wildlife Research Institute's Buddy Temple Wildlife Pathology and Diagnostic Building for necropsy or individually transferred to quart-sized freezer bags and placed in a cooler containing a mixture of dry ice and ethanol for the purpose of fast-freezing (Glass et al., 2002). Host species were collected in accordance with established permits issued by the Texas Parks and Wildlife Department and the U.S. Fish and Wildlife Service, and approved by the Texas A&M University–Kingsville Institutional Animal Care and Use Committee.

### Helminth collection, processing, and identification

If frozen, columbids were thawed at room temperature or by running warm water over the freezer bag containing the carcasses. Once thawed, each bird was divided into carcass and viscera. The following microhabitats were examined under a dissecting microscope (×9–40): eye surface and nictating membrane, nasal cavity, nasal sinus, suborbital sinus, and brain. The viscera were divided into the following microhabitats: trachea, lungs, heart, kidney, liver, esophagus, proventriculus, gizzard, gall bladder, pancreas, spleen, intestine (divided into duodenum, jejunum, and ileum), cloaca, female reproductive tract, mesenteric veins, bursa (when present), and miscellaneous wash (rinse from the freezer bag).

Nematodes were fixed in glacial acetic acid and stored in 70% ethanol and 8% glycerin. Cestodes were heat relaxed by flaming or fixed in acetic acid–formalin–ethanol (AFA) and stored in 70% ethanol. Representative cestodes were stained using Semichon's acid carmine or Harris' hematoxylin and eosin and mounted with Damar Balsam (Damar xylene) for identification. Identification of cestodes followed the taxonomic key of Schmidt (1986) and original species descriptions. Identification of nematodes followed original descriptions. Once identified, specimens of each helminth species were quantified. Representative specimens were deposited into the Harold W. Manter Parasite Collection, University of Nebraska State Museum, Lincoln, Nebraska (accession numbers P-2008-878-48958 to P-220-878-48958).

### Statistical analyses

Definitions of parasitological terms follow that of Bush et al. (1997). Common, intermediate, and rare helminth species are arbitrarily defined as those that occurred in >75, 25–75, and <25% of hosts sampled, respectively. A chi-square test (SAS Institute, Inc., 1990) was used to analyze the prevalence of common and intermediate species between host species, and within host species, by host age and gender. Abundance data were rank-transformed prior to parametric statistical analysis (Conover and Iman, 1981). Rank abundance values were examined for the main (species, age, and gender) and interaction effect variables with the general linear model (GLM) of analysis of variance (ANOVA; SAS Institute, Inc., 1990). For significant ANOVA models, multiple comparisons of main effects variables $\geq 3$ were made using Tukey's studentized range test (Cochran and Cox, 1957). Least squares mean procedure was used to assess significant interaction effects (LSM; SAS Institute, Inc., 1990). All tests were considered significant at $P \leq 0.05$. Descriptive summary statistics of raw data are presented as the mean ±1 standard error (SE).

Three measures of community were utilized—the percent similarity index ($PS_i$; Krebs, 1989) was used to compare proportions of helminth species between host component communities; the Jaccard's index ($J_i$; Jaccard, 1912; Magurran, 1988) evaluated the similarity of shared species between host species; and the numerical dominance index ($D_i$; Leong and Holmes, 1981) was used to assess numerical dominance relationships of helminth species (by dividing the total abundance of each helminth taxa by the total abundance of all helminths in the host species, and multiplying the quotient by 100).

## RESULTS

## General

Twelve species of helminths (9 nematodes and 3 cestodes) were identified from the 248 columbids examined, representing 486 helminth individuals (Table I). Tables I, II, and III present helminth prevalence, intensity, and abundance values for each host species examined. Helminths occurred in 6 microhabitats (proventriculus, jejunum, duodenum, ileum, heart, and liver), of which the jejunum was the most commonly occupied. Nematodes numerically dominated the component community in all host species (Table I).

### Infracommunity and component community overview by host species

*Rock pigeon:* Sixty percent of 60 RPs were infected with helminths, representing 5 species (2 nematodes and 3 cestodes); 193 helminth individuals were found, averaging 3.2 ± 1.4 helminth individuals per host individual. Nematodes dominated numerically (60% of total helminths), followed by cestodes (40%). The intestine was the most commonly occupied microhabitat. However, the proventriculus was occupied with 2 nematode species (*Tetrameres* sp. and *Dispharynx nasuta*) in 1 host individual, and 1 nematode species (*T. americana*) in another host individual. All other microhabitats were unoccupied (Table I). The distribution patterns of infracommunity species richness ranged from 1 to 3 species per infected host. Nematodes were not found in the intestine of this host. The 2 nematode species identified, *D. nasuta* and *T. americana*, are site specific to the proventriculus.

One cestode, *Hymenolepis* sp., was the most prevalent helminth species, which occurred in 30% of RPs examined and accounted for 27% of all helminth individuals in this host. The remaining species were rare and contributed minimally to the component community. Prevalence of *Hymenolepis* sp. was higher ($P$ = 0.0003) in adults than juveniles (49% and 4%, respectively); however, there was no difference ($P$ = 0.69) between males and females (32% and 28%, respectively). Likewise, prevalence of *Skrjabinia bonini* was higher ($P$ = 0.01) in adults than juveniles (26% and 0%, respectively); however, there was no difference ($P$ = 0.54) between males and females (10% and 19%, respectively). Rank abundance of *Hymenolepis* sp. was lower ($P$ = 0.0003) in juveniles, compared to adults. However, rank abundance was similar ($P$ = 0.6) with respect to host gender. Prevalence and abundance values for the remaining helminth species identified from this host were too low to make comparisons by host age or gender.

*Eurasian collared-dove:* Twenty-seven percent of 60 ECDs were infected; 3 species (1 nematode and 2 cestodes) were found. Thirty helminth individuals were recovered, averaging 0.5 ± 0.1 helminth individuals per infected host. Nematodes dominated numerically (87% of total helminths), followed by cestodes (13%). The intestine was the only occupied microhabitat.

*Ascaridia columbae* was the most prevalent helminth species, which occurred in 20% of ECDs examined, and this species accounted for 87% of all helminth individuals at the component community level (Tables I, III). The remaining species were rare and contributed minimally to the component community. Prevalence and abundance values for the remaining helminth species identified from this host were too low to make comparisons by host age or gender.

*Mourning dove:* Examination of 60 MDs revealed 37% were infected, and 6 species of helminths (4 nematodes and 2 cestodes) were found; 37 helminth individuals were present, averaging 0.6 ± 0.1 helminth individuals per host. Nematode and cestode

TABLE I. Helminth prevalence values from south Texas columbids (summer 2006).

| Helminth species | Location* | RP (N = 60) | MD (N = 60) | WWD (N = 60) | ECD (N = 60) | CGD (N = 60) | ID (N = 48) |
|---|---|---|---|---|---|---|---|
| Nematoda | | | | | | | |
| *Ascaridia columbae* | D, J, I | 0 | 0 | 5/8.0% | 12/20.0% | 6/10.0% | 2/4.2% |
| *Splendidofilaria wehri* | L | 0 | 0 | 0 | 0 | 2/3.0% | 0 |
| *Tetrameres* sp. | P | 2/3.0% | 0 | 0 | 0 | 0 | 0 |
| *Dispharynx nasuta* | P | 1/2.0% | 0 | 1/2.0% | 0 | 0 | 0 |
| *Ornithostrongylus minutus* | D, J, I, DW | 0 | 0 | 3/5.0% | 0 | 18/30.0% | 0 |
| *Ornithostrongylus quadriradiatus* | D, J, I, DW | 0 | 3/5.0% | 2/3.0% | 0 | 3/5.0% | 0 |
| *Ornithostrongylus* sp. | D, J, I, DW | 0 | 5/8.0% | 0 | 0 | 2/3.0% | 0 |
| *Oswaldostrongylus* sp. | D, J, I, DW | 0 | 2/3.0% | 3/5.0% | 0 | 3/5.0% | 0 |
| *Aproctella stoddardi* | H | 0 | 1/2.0% | 0 | 0 | 3/5.0% | 0 |
| Cestoda | | | | | | | |
| *Killigrewia delafondi* | D, J | 3/5.0% | 8/13.0% | 12/20.0% | 3/5.0% | 7/12.0% | 0 |
| *Skrjabinia bonini* | D, J | 9/15.0% | 0 | 1/2.0% | 0 | 1/2.0% | 0 |
| *Hymenolepis* sp. | D, J, I, DW | 18/30.0% | 5/8.0% | 0 | 1/2.0% | 7/12.0% | 0 |

RP = rock pigeon, MD = mourning dove, WWD = white-winged dove, ECD = Eurasian collared-dove, CGD = common ground dove, and ID = Inca dove.
* DW = decantation wash; D = duodenum; J = jejunum; I = ileum; H = heart; P = proventriculus; L = liver.

infections were comparable (51% and 49%, respectively). The intestine was the most commonly occupied microhabitat. However, the heart was occupied with 1 nematode species (*Aproctella stoddardi*) in 1 host individual. All other microhabitats were unoccupied. *Oswaldostrongylus* sp. is a new host record.

The cestode *Killigrewia delafondi* was the most prevalent helminth species; it occurred in 13% of MDs examined, accounting for 27% of all helminth individuals at the component community level (Tables I, III). The remaining species were rare (<8% prevalence) and contributed minimally to the component community. Prevalence and abundance values for the remaining helminth species were too low to make comparisons by host age or gender.

*White-winged dove:* Examination of 60 WWDs revealed 37% were infected; 7 helminth species (5 nematodes and 2 cestodes) were found; 62 helminth individuals were present, averaging 1.0 ± 0.3 helminth individuals per host. Nematodes dominated numerically (65% of total helminths), followed by cestodes (36%). The intestine was the most commonly occupied microhabitat, whereas the proventriculus was occupied with 1 nematode species, *D. nasuta*, in 1 host individual. All other microhabitats were without parasites. *Oswaldostrongylus* sp. and *S. bonini* are new host records.

Though rare, the cestode *K. delafondi* was the most prevalent helminth species, which occurred in 20% of WWDs examined and accounted for 44% of all helminth individuals at the component community level (Tables I, III). The remaining species were also rare and contributed minimally to the component community. Prevalence of *K. delafondi* was higher ($P = 0.0001$) in adults than juveniles (40% and 0%, respectively); however, there was no difference ($P = 0.30$) between males and females (26% and 15%, respectively). Prevalence and abundance values for all other helminth species were too low to make comparisons by host age or gender.

*Common ground dove:* Examination of 60 CGDs revealed 60% were infected; 10 species of helminths (7 nematode and 3 cestode)

TABLE II. Helminth intensity values (mean ± standard error followed by the range in parentheses) from south Texas columbids (summer 2006).

| Helminth species | RP (N = 60) | MD (N = 60) | WWD (N = 60) | ECD (N = 60) | CGD (N = 60) | ID (N = 48) |
|---|---|---|---|---|---|---|
| Nematoda | | | | | | |
| *Ascaridia columbae* | | | 2.4 ± 0.8 (1–5) | 2.2 ± 0.5 (1–6) | 4.3± 1.3 (1–10) | 3.5 ± 2.5 (1–6) |
| *Splendidofilaria wehri* | | | | | 3.0 ± 1.0 (2–4) | |
| *Tetrameres* sp. | 53.0 ± 21.5 (32–75) | | | | | |
| *Dispharynx nasuta* | 9 (9) | | 5 (5) | | | |
| *Ornithostrongylus minutus* | | | 2.3 ± 1.3 (1–5) | | 4.8 ± 1.3 (1–22) | |
| *Ornithostrongylus quadriradiatus* | | 2.0 ± 0.6 (1–3) | 2.5 ± 1.5 (1–4) | | 2.0 ± 1 (1–4) | |
| *Ornithostrongylus* sp. | | 1.4 ± 0.4 (1–3) | | | 1 (1) | |
| *Oswaldostrongylus* sp. | | 2 (2) | 3.7 ± 0.7 (3–5) | | 1.3± 0.3 (1–2) | |
| *Aproctella stoddardi* | | 2 (2) | | | 2 (2) | |
| Cestoda | | | | | | |
| *Killigrewia delafondi* | 1 (1) | 1.3 ± 0.2 (1–2) | 1.8 ± 0.5 (1–6) | 1 (1) | 1.1± 0.1 (1–2) | |
| *Skrjabinia bonini* | 2.4 ± 0.7 (1–7) | | 1 (1) | | 1 (1) | |
| *Hymenolepis* sp. | 2.8 ± 0.4 (1–9) | 1.6 ± 0.2 (1–2) | | 1 (1) | 1.4± 0.3 (1–3) | |

RP = rock pigeon, MD = mourning dove, WWD = white-winged dove, ECD = Eurasian collared-dove, CGD = common ground dove, and ID = Inca dove.

TABLE III. Helminth abundance values (mean ± standard error followed by total helminths in parentheses) from south Texas columbids (summer 2006).

| Helminth species | RP (N = 60) | MD 9 (N = 60) | WWD (N = 60) | ECD (N = 60) | CGD (N = 60) | ID (N = 48) |
|---|---|---|---|---|---|---|
| Nematoda | | | | | | |
| *Ascaridia columbae* | | | 0.2 ± 0.1 (12) | 0.4 ± 0.1 (26) | 0.4 ± 0.2 (26) | 0.1 ± 0.1 (7) |
| *Splendidofilaria wehri* | | | | | 0.1 ± 0.1 (6) | |
| *Tetrameres* sp. | 1.7 ± 1.4 (107) | | | | | |
| *Dispharynx nasuta* | 0.2 ± 0.2 (9) | | 0.1 ± 0.1 (5) | | | |
| *Ornithostrongylus minutus* | | | 0.1 ± 0.1 (7) | | 1. 4 ± 0.5 (88) | |
| *Ornithostrongylus quadriradiatus* | | 0.1 ± 0.1 (6) | 0.1 ± 0.1 (5) | | 0.1 ± 0.1 (6) | |
| *Ornithostrongylus* sp. | | 0.1 ± 0.1 (7) | | | <0.1 ± <0.1 (2) | |
| *Oswaldostrongylus* sp. | | 0.1 ± 0.1 (4) | 0.2 ± 0.1 (11) | | 0.1 ± <0.1 (4) | |
| *Aproctella stoddardi* | | <0.1 ± <0.1 (2) | | | 0.1 ± 0.1 (6) | |
| Cestoda | | | | | | |
| *Killigrewia delafondi* | 0.1 ± <0.1 (3) | 0.2 ± 0.1 (10) | 0.4 ± 0.1 (21) | 0.1 ± <0.1 (3) | 0.1 ± 01 (8) | |
| *Skrjabinia bonini* | 0.4 ± 0.2 (22) | | <0.1 ± <0.1 (1) | | <0.1 ± <0.1 (1) | |
| *Hymenolepis* sp. | 0.7 ± 0.2 (52) | 0.1 ± 0.1 (8) | | <0.1 ± 0.1 (1) | 0.2 ± 0.1 (10) | |

RP = rock pigeon, MD = mourning dove, WWD = white-winged dove, ECD = Eurasian collared-dove, CGD = common ground dove, and ID = Inca dove.

were found; 157 helminth individuals were found and averaged 2.6 ± 0.5 helminth individuals per host. Nematodes dominated numerically (88% of total helminths), followed by cestodes (12%). The intestine was the most commonly occupied microhabitat. The heart and liver were occupied with 1 species of nematode each (*Skrjabinia wehri* and *A. stoddardi*, respectively). All other microhabitats were unoccupied. *Ascaridia columbae*, *S. wehri*, *Ornithostrongylus minutus*, *Oswaldostrongylus* sp., *K. delafondi*, and *S. bonini* are new host records.

*Ornithostrongylus minutus* was the most prevalent species, which occurred in 30% of common ground doves examined and accounted for 56% of all helminth individuals at the component community level (Tables I, III). The remaining species were rare and contributed minimally to the component community. Prevalence and abundance values for all other helminth species identified from this host were too low to make comparisons by host age or gender.

*Inca dove: Ascaridia columbae* was the only species found, and it occurred exclusively in the jejunum. This species was rare, occurring in 4% of the birds (Tables I, III) and had a mean abundance of 0.2 ± 0.1. Infection only occurred in adults, with males and females infected equally (2% each). *Ascaridia columbae* is a new host record.

## Helminth community analyses

Based on $PS_i$ and $J_i$, helminth component communities were dissimilar, and the number of shared helminth species varied among host species (Table IV). Helminth component communities among hosts differed in several unique ways. First, the 2 exotic hosts (RP and ECD) had strong dissimilarities ($PS_i = 5$, $J_i = 3$). Second, ID and RP, which are both urban-dwelling species (but forage in different habitat types), were completely dissimilar ($PS_i = 0$, $J_i = 0$). Third, ID was completely dissimilar ($PS_i = 0$, $J_i = 0$) to urban- and rural-feeding dove species (MD and CGD). Finally, 3 urban/rural species, MD, CGD, and WWD, had the most similarities within their helminth communities (MD and WWD 46%; WWD and CGD 41%) based on $PS_i$ (Table IV). The communities that displayed the highest $PS_i$ were those that shared the same cestode species.

Table V presents $D_i$ values generated for all helminth species collected from all 6 host species. The nematode *T. americana* numerically dominated (56%) the RP helminth community. However, this was due to high intensity of infection in 2 hosts. The cestode, *Hymenolepis* sp. had a $D_i$ value of 27% and was more evenly distributed among RPs. The nematode *A. columbae* numerically dominated (87%) the ECD helminth community. Two cestode species with a combined $D_i$ value of 13% comprised the rest of the helminth community. The MD helminth community was numerically dominated by the cestode *K. delafondi* (27%). Cestode and nematode species were evenly distributed within this helminth community (49% and 51%, respectively). Although nematodes numerically dominated as a group within the WWD helminth community (65%), the cestode *K. delafondi* individually dominated (34%). Nematodes dominated the CGD helminth

TABLE IV. Helminth community analysis by columbid species using percent similarity index ($PS_i$) and Jaccard's index ($J_i$, in parentheses) in south Texas columbids (summer 2006).

| Dove species | ECD (N = 60) | MD (N = 60) | WWD (N = 60) | ID (N = 48) | CGD (N = 60) |
|---|---|---|---|---|---|
| RP | 5* (3†) | 24 (22) | 9 (33) | 0 (0) | 9 (25) |
| ECD | | 13 (29) | 29 (25) | 7 (33) | 26 (30) |
| MD | | | 46 (30) | 0 (0) | 24 (60) |
| WWD | | | | 19 (14) | 41 (51) |
| ID | | | | | 0 (0) |

RP = rock pigeon, MD = mourning dove, WWD = white-winged dove, ECD = Eurasian collared-dove, CGD = common ground dove, and ID = Inca dove.
* Values for $PS_i$ range from 0 to 100, where 0 = completely dissimilar communities, and 100 = completely similar communities.
† Values for $J_i$ range from 0 to 100, where 0 = completely dissimilar communities, and 100 = completely similar communities.

TABLE V. The numerical dominance index ($D_i$) values generated for helminth species from south Texas columbids (summer 2006).

| Helminth species | RP (N = 60) | MD (N = 60) | WWD (N = 60) | ECD (N = 60) | CGD (N = 60) | ID (N = 48) |
|---|---|---|---|---|---|---|
| *Ascaridia columbae* | 0 | 0 | 19.4 | 86.7 | 16.6 | 100.0 |
| *Splendidofilaria wehri* | 0 | 0 | 0 | 0 | 3.8 | 0 |
| *Tetrameres* sp. | 55.4 | 0 | 0 | 0 | 0 | 0 |
| *Dispharynx nasuta* | 4.7 | 0 | 8.1 | 0 | 0 | 0 |
| *Ornithostrongylus minutus* | 0 | 0 | 11.3 | 0 | 56.1 | 0 |
| *Ornithostrongylus quadriradiatus* | 0 | 16.2 | 8.1 | 0 | 3.8 | 0 |
| *Ornithostrongylus* sp. | 0 | 18.9 | 0 | 0 | 1.3 | 0 |
| *Oswaldostrongylus* sp. | 0 | 10.8 | 17.7 | 0 | 2.5 | 0 |
| *Aproctella stoddardi* | 0 | 5.4 | 0 | 0 | 3.8 | 0 |
| *Killigrewia delafondi* | 1.6 | 27.0 | 33.9 | 10.0 | 5.1 | 0 |
| *Skrjabinia bonini* | 11.3 | 0 | 1.6 | 0 | 0.6 | 0 |
| *Hymenolepis* sp. | 26.9 | 21.6 | 0 | 3.3 | 6.4 | 0 |

RP = rock pigeon, MD = mourning dove, WWD = white-winged dove, ECD = Eurasian collared-dove, CGD = common ground dove, and ID = Inca dove.

community (87%), with *O. minutus* accounting for 56% of the helminth individuals (Table V).

## DISCUSSION

Helminth community studies that focus on a single host species often ignore the potential influences of phylogenetically related co-occurring hosts. Consequently, interactions by hosts and their helminths are not fully understood. In the present study, helminth communities were simultaneously examined within a regionally co-occurring columbid community (hosts occurring across a spatial environmental gradient), with some species co-occurring locally.

Helminth communities seemed to reflect habitat utilization and foraging site choice. An example of this can be seen when comparing the parasite communities from RPs in Old World and New World studies. Old world RPs (Tables BI, BII, BIII) are infected with component communities comparable to those of New World MDs and WWDs (Table V; Tables BI, BII, BIII). However, the RP population collected during this study reflects a parasite community suggestive of the local environment in which they forage/take grit. The local RP population in the Kingsville, Texas, area supplements foraging twice daily at a local cattle feed yard, thereby decreasing exposure probabilities to direct life-cycle nematodes (uninhabitable soil conditions) that could occur in other columbids foraging at natural feeding sites. However, RPs at the feed yard were exposed to and consumed large quantities of various grain beetle species, as well as the juvenile face fly (*Musca autumnalis*) and increased their exposure probability to *Hymenolepis* sp. infections (A. Smith, pers. obs.; Table I). Mourning doves and WWDs are habitat generalists, and so they are exposed to a wider array of direct life-cycle helminths and intermediate hosts (Table V). Mourning doves are well adapted to urban, suburban, and rural areas, giving them the widest foraging breadth of all hosts examined. However, most MDs examined in this study were collected from rural areas and often within similar habitats as the CGD and WWDs. In this case, our collection methods may, in part, be responsible for the observed helminth communities. Helminth communities collected from hosts residing in permanent environmental habitats (CGD is strictly rural, and ID is strictly urban) had predictable and completely dissimilar communities. However, helminth communities collected from hosts that co-occur along the environmental gradient (WWD, MD, ECD, and RP) had unpredictable and overlapping helminth communities (Tables I, IV). Future studies on such systems should include close evaluation of host habitat use, foraging strategies, and diet to aid in interpretation helminth communities. In all host species, component communities were dominated by "columbid" nematodes (Table V). Because columbids are ground gleaners, the numerical domination by direct life-cycle nematodes is apparent. Of the 9 nematode species taken from all host species, 7 have direct life cycles. The exceptions, *Tetrameres* sp. and *D. nasuta*, infecting RP, use snails and isopods, respectively, as intermediate hosts, which likely are accidentally ingested. The prevalence, abundance, and numerical dominance of cestodes among most of the host species were relatively low, reflecting host foraging tendencies toward granivory. The prevalence of *K. delafondi* in WWD (20.0%) and MD (13.0%), and *Hymenolepis* sp. in RP (30.0%) may be explained, respectively, by each species' tendency to feed in areas where intermediate hosts are abundant (rural areas and cattle feed lots). Two host species (RP and ECD) examined in this study were introduced into North America in the seventeenth century and ca. 1972, respectively. The RP has a longer evolutionary history with the environment (~400 yr) compared to that of ECD (~38 yr). Because ECD is the newest columbid to North America, and very few helminthological studies have been conducted on this species (Forrester and Spalding, 2003), further investigations are needed as the ECD expands its range across North America. Torchin et al. (2003) suggested that parasite component communities in introduced hosts are typically species poor for several reasons. First, for indirect life-cycle parasites, the proper invertebrate hosts required for transmission may be absent from the new habitat. Second, there may be insufficient numbers in a founding population to establish itself into the new habitat. Third, as parasites are lost upon host introduction, newly formed component communities may be gained via host switching from sympatric host species, but these do not, on average, compensate for parasites lost. The parasite communities of RPs and ECDs surveyed in this study reflect the suggestions proposed by Torchin et al. (2003). Helminthological surveys of RPs and ECDs are rare in North America. However, it is clear that endemic helminth species are being acquired by these invasive hosts at a rate consistent with time spent in their new environment. Tables BI, BII, and BIII allow for easy comparison of helminths reported from Old and New World introduced hosts. For example, 36 nematode species are currently reported from Old World and New World RP populations. Of these, 30 species are reported from Old World populations, 12 are reported from New World populations, and 6 are shared (occur in both Old and New World RPs). Likewise, 10 nematode species are currently reported from Old and New World ECD populations. Of these, 4 species are reported from Old World populations, and 6 are reported from New World populations, but there have been no reports of shared nematode species between Old and New World ECD populations. It is likely, however, that as ECD continues to establish permanent populations across North America, it will acquire native helminth species from local sympatric host species.

In the present study, helminth communities were depauperate in terms of species richness (1–10 helminth species) and numbers of individuals (1–75), reflecting minimal exposure to both direct and indirect helminth infective stages within the environment, which is likely attributable to the hosts' granivorous diet. However, host species such as RP that exploit man-made foraging sites (cattle feed lots) substantially increased their exposure to cestodes that occurred at these sites, whereas IDs (which exploit urban birdfeeders) were infected with only *A. columbae*. We conclude that although hosts in this study co-occur regionally, there is sufficient ecological separation locally (likely in terms of both roosting/nesting sites and foraging habits) to ultimately result in differing helminth communities within these 6 closely related host species.

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## APPENDIX A—PATTERNS OF DISTRIBUTION, HABITAT RANGE, FEEDING HABITS, AND FORAGING BEHAVIOR FOR EACH HOST SPECIES (RP, MD, WWD, ECD, CGD, AND ID) EXAMINED

*Rock pigeon:* The RP originated in Europe and was introduced into North America by early colonists in the seventeenth century. Now nearly cosmopolitan, the RP's habitat encompasses open and semi-open environments, including agricultural and urban areas (Johnston, 1992). In south Texas, this is a gregarious species that roosts/nests in urban to suburban areas but often exploits cattle feed yards and grain elevators. Numerous studies exist addressing the helminths of RPs residing in the Old World; however, few studies have been published for the New World populations (Appendix B).

*Mourning dove:* The MD has an extensive New World geographical distribution ranging from South Canada and throughout North America. This is a rural, suburban, and urban species in which generalist behavior has allowed it to exploit habitats altered by humans (Baskett et al., 1993). Foraging behavior includes feeding almost exclusively on the ground in all 3 areas, but individuals will also utilize elevated bird feeders. Several well-documented helminthological surveys have been conducted on MDs (Barrows and Hays, 1977; Lee et al., 2004; Appendix B) due, in part, to their status and economic value as a game bird species.

*White-winged dove:* The WWD has a geographic distribution ranging from the southernmost areas of the United States to Mexico and is partially migratory through Central America and the West Indies (Schwertner et al., 2002). This species has a tendency to exploit areas associated with human habitation in areas outside their native range (Cottam et al., 1968). Foraging habits differ from MDs in that this species will feed on food sources that are elevated above ground in urban and suburban areas. Few documented helminthological surveys (Appendix B) have been conducted on this species because of its limited geographical range.

*Eurasian collared-dove:* The ECD originated in India and was subsequently introduced into North America in the mid 1970s (Ramagosa, 2002). Since its introduction, this dove has spread rapidly across North America. Its habitat includes rural and suburban areas, but it is rapidly expanding its range to include urban/agricultural habitats. Foraging habits include ground, waste, and stored grain (including animal feed from agriculture areas), but individuals will also take seeds from elevated bird feeders (Ramagosa, 2002). The only published study from North America (Bean et al., 2005) (also see Appendix B) examined the helminths of this species in Florida.

*Common ground dove:* The CGD is found throughout the southernmost tier of the United States from Florida to California, the West Indies, Mexico, and much of Central America, and the northern third of South America (Bowman, 2002). This species is strongly associated with arid, early successional open woodlands and shrub or scrub habitats (Bowman, 2002). As a rural ground gleaner, CGD individuals tend toward areas of bare, sandy soil, consuming large quantities of small, native and exotic seeds. Ground doves do not forage in agricultural, urban, or suburban areas and have foraging tendencies and behaviors that parallel that of the rural-feeding MD. To date, no complete helminthological survey has been conducted for this species (see partial survey in Stabler, 1962; Appendix B).

*Inca dove:* The ID is a native columbid of Mexico, northern Central America, and the southwestern United States (Mueller, 1992). It is a strictly urban species that almost exclusively exploits residential backyard birdfeeders and birdbaths. To date, no complete helminthological survey has been conducted for this dove species (Appendix B).

# APPENDIX B

TABLE BI. Species of nematodes found in both Old World doves (ECD and RP) and New World doves (MD, WWD, GD, and ID).

| | ECD | | RP | | | | | |
|---|---|---|---|---|---|---|---|---|
| Helminth taxa | Old | New | Old | New | MD | WWD | CGD | ID |
| *Acuaria hamulosa* | | | + | | | | | |
| *Amidostomum anseris* | + | | | | | | | |
| *Aonchotheca caudinflata** | + | | + | | | | | |
| *Aproctella stoddardi* | | + | | | + | + | + | |
| *Ascaridia columbae** | | + | + | + | + | + | + | |
| *Ascaridia galli* | | | + | | | | | |
| *Baruscapillaria obsignata* | + | | + | | | | | |
| *Baylisascaris procyonis* | | | | | + | | | |
| *Baylisascaris* sp. | | | | | + | | | |
| *Brachylecithum filum* | | | + | | | | | |
| *Capillaria annulata* | | | + | | | | | |
| *Capillaria bursata* | | | + | | | | | |
| *Capillaria caudinflata* | | | + | | | | | |
| *Capillaria columbae* | | | + | + | | | | |
| *Capillaria gallinae* | | | + | | | | | |
| *Capillaria obsignata** | | + | + | | + | + | | |
| *Capillaria tenuissimum* | | | | + | | | | |
| *Dispharynx nasuta* | | + | + | + | + | + | + | |
| *Dispharynx spiralis* | | | + | + | | | | |
| *Eulimdana clava** | | | + | | | | | |
| *Excisa columbi** | | | + | | | | | |
| *Filaria* sp. | | | + | | | | | |
| *Hadjelia* sp.* | | | + | | | | | |
| *Heterakis maculosa* | | | + | + | | | | |
| *Microtetrameres helix* | | | | + | | | | |
| *Ornithostrongylus crami* | | | | | + | | | |
| *Ornithostrongylus iheringi* | | | | | + | + | | |
| *Ornithostrongylus quadriradiatus* | | | + | + | + | + | + | + |
| *Ornithostrongylus minutus* | | | | | + | + | | |
| *Ornithostrongylus* sp. | | + | | | + | + | | |
| *Pelecitus* sp. | | | + | | | | | |
| *Postharmostomum commutatum* | | | + | | | | | |
| *Pterothominx caudinflata** | + | | + | | | | | |
| *Pterothominx wavilovoi*† | | | + | | | | | |
| *Splendidofilaria* sp. | | + | | | | + | | |
| *Strongyloides avium* | | | + | | | | | |
| *Strongyloides* sp. | | | + | | | | | |
| *Strongyloidea complex* | | | | | | + | | |
| *Syngamus tracheae* | | | + | | | | | |
| *Synhimantus spiralis* | | | + | | | | | |
| *Tetrameres columbicola* | | | | + | + | + | | |
| *Tetrameres americanus* | | + | | + | | | | |
| *Tetrameres fissispina** | | | + | | | | | |
| *Trichosoma tenuissimum* | | | | + | | | | |
| *Trichostrongylus* spp. | | | | + | | | | |
| Total | 4 | 7 | 29 | 12 | 12 | 11 | 4 | 1 |

RP = rock pigeon, MD = mourning dove, WWD = white-winged dove, ECD = Eurasian collared-dove, CGD = common ground dove, and ID = Inca dove.
* Nematode described from *Columba livia domestica* and *Columba livia*.
† Nematode described from *Columba livia domestica* only.
New World sources: Mukherjee (1964); Rutherford and Black (1974); Conti and Forrester (1981); Canadian Council on Animal Care (1984); Bennett and Peirce (1990); Johnston (1992); Mueller (1992); Mirachi and Baskett (1994); Gicik and Arslan (1999); Erwin et al. (2000); Glass et al. (2002); Schwertner et al. (2002); Forrester and Spalding (2003); Foronda et al. (2004); Bean et al. (2005).
Old World sources: Mukherjee (1964); Rutherford and Black (1974); Gicik and Arslan (1999); Foronda et al. (2004); and museum listings.

TABLE BII. Species of trematodes found in both Old World doves (ECD and RP) and New World doves (MD, WWD, GD, and ID).

| Helminth taxa | ECD Old | ECD New | RP Old | RP New | MD | WWD | GD | ID |
|---|---|---|---|---|---|---|---|---|
| *Austrobilharzia penneri* | | | | + | | | | |
| *Brachylaima columbae* | | | + | | | | | |
| *Brachylaima degiustii* | | | + | + | | | | |
| *Brachylaima fuscatus* | + | + | + | | | | | |
| *Brachylaima mesostoma* | | | + | | | | | |
| *Brachylaima mazzanti* | | + | + | | | + | | |
| *Brachylaima nicolli* | | | + | | | | | |
| *Brachylaima* sp. | | | + | + | + | + | | |
| *Cotylurus cornutus* | | | + | | | | | |
| *Echinoparyphium paraulum* | | | + | | | | | |
| *Echinoparyphium recurvatum* | | | + | | | | | |
| *Echinoparyphium schulzi* | | | + | | | | | |
| *Echinostoma echinatum* | | | + | | | | | |
| *Echinostoma revolutum* | | | + | + | + | | | |
| *Glaphyrostomum indicum* | | | + | | | | | |
| *Glaphyrostomum* sp. | | | | | | + | | |
| *Hypoderaeum conoideum* | | | + | | | | | |
| *Metechinostoma amurensis* | | | + | | | | | |
| *Pharyngostomum cordatum* | | | + | | | | | |
| *Philopthalmus alii* | + | | | | | | | |
| *Philopthalmus columbae* | | | + | | | | | |
| *Philopthalmus gralli* | | | | | | + | | |
| *Philopthalmus lucipetus* | | | + | | | | | |
| *Prosthogonimus ovatus* | | | + | | | | | |
| *Prosthogonimus pellucidus* | | | + | | | | | |
| *Skrjabinus petrowi* | | | + | | | | | |
| *Tanaisia bragai* | | + | + | | + | + | | |
| *Tanaisia domestica* | | | | + | | | | |
| Total | 2 | 3 | 22 | 5 | 3 | 5 | 0 | 0 |

RP = rock pigeon, MD = mourning dove, WWD = white-winged dove, ECD = Eurasian collared-dove, CGD = common ground dove, and ID = Inca dove.
New World sources: Mukherjee (1964); Rutherford and Black (1974); Conti and Forrester (1981); Canadian Council on Animal Care (1984); Bennett and Peirce (1990); Johnston (1992); Mueller (1992); Mirachi and Basket (1994); Gicik and Arslan (1999); Erwin et al. (2000); Glass et al. (2002); Schwertner et al. (2002); Forrester and Spalding (2003); Foronda et al. (2004); Bean et al. (2005).
Old World sources: Mukherjee (1964); Rutherford and Black (1974); Gicik and Arslan (1999); Foronda et al. (2004); and museum listings.

TABLE BIII. Species of cestodes found in both Old World doves (ECD and RP) and New World doves (MD, WWD, GD, and ID).

| | ECD | | RP | | | | | |
|---|---|---|---|---|---|---|---|---|
| Helminth taxa | Old | New | Old | New | MD | WWD | GD | ID |
| *Aoorina nakayamai** | | | + | | | | | |
| *Choanotaenia infundibulum* | | | + | | | | | |
| *Cotugnia chauhani*† | | | + | | | | | |
| *Cotugnia cuteata* | + | | | | | | | |
| *Cotugnia intermedia* | | | + | | | | | |
| *Cotugnia manishae* | | | + | | | | | |
| *Cotugnia satpuliensis* | | | + | | | | | |
| *Cotugnia visakhapatnamensis* | | | + | | | | | |
| *Davainea crassula* | | | + | | | | | |
| *Davainea jalnaensis* | | | + | | | | | |
| *Davainae proglottina* | | | + | | | | | |
| *Davainae retharei* | + | | | | | | | |
| *Diorchis magnicirrosa* | + | | | | | | | |
| *Diorchis moghei* | | | + | | | | | |
| *Fuhrmannetta crassula* | | + | | | | | | |
| *Hymenolepis clausa* | | | + | | | | | |
| *Hymenolepis columbae* | | | + | | | | | |
| *Hymenolepis joyeuxi* | | | + | | | | | |
| *Hymenolepis macracanthos* | | | + | | | | | |
| *Hymenolepis rugosa* | | | + | | | | | |
| *Hymenolepis serrata* | | | + | | | | | |
| *Hymenolepis sphenocephala* | | + | | | | | | |
| *Hymenolepis streptopeliae* | | | + | | | | | |
| *Hymenolepis* sp. | | + | | | + | + | | |
| *Killigrewia delafondi* | + | + | + | + | + | + | | |
| *Killigrewia frivola*‡ | | | + | | | | | |
| *Laterorchites yamaguti* | | | + | | | | | |
| *Ophryocotylus oraiensis* | | | + | | | | | |
| *Paradicranotaenia anormalis* | | | + | | | | | |
| *Passerilepis streptopeliae* | + | | | | | | | |
| *Prosthorhynchus transverses* | | | + | | | | | |
| *Pulluterina karachiensis* | | | + | | | | | |
| *Raillietina beppuensis** | | | + | | | | | |
| *Raillietina bonini* | | | + | | | | | |
| *Raillietina buckleyi* | + | | | | | | | |
| *Raillietina bungoensis** | | | + | | | | | |
| *Raillietina carpophagi** | | | + | | | | | |
| *Raillietina cesticilus* | | | + | | | | | |
| *Raillietina echinobothrida* | | | + | | | | | |
| *Raillietina fragilis* | | | + | | | | | |
| *Raillietina francolini* | | | + | | | | | |
| *Raillietina fuhrmanni* | + | | | | | | | |
| *Raillietina japonensis* | | | + | | | | | |
| *Raillietina johri* | | | + | | | | | |
| *Raillietina joyeuxi* | | | + | | | | | |
| *Raillietina kaimonjiensis** | | | + | | | | | |
| *Raillietina kantipura* | | | + | | | | | |
| *Raillietina kirghizica* | | | + | | | | | |
| *Raillietina korkei* | | | + | | | | | |
| *Raillietina kyushuensis* | | | + | | | | | |
| *Raillietina micracantha*‡ | | | + | | | | | |
| *Raillietina michaelseni* | | | + | | | | | |
| *Raillietina nagpurensis* | + | | + | | | | | |
| *Raillietina paucitesticulata* | | | + | | | | | |
| *Raillietina polychalix* | | | + | | | | | |
| *Raillietina rugosa* | | | + | | | | | |
| *Raillietina sinensis** | | | | | | | | |
| *Raillietina tetragona* | | | + | | | | | |
| *Raillietina tokyoensis** | | | + | | | | | |

(Table continued)

TABLE BIII. Continued.

| Helminth taxa | ECD Old | ECD New | RP Old | RP New | MD | WWD | GD | ID |
|---|---|---|---|---|---|---|---|---|
| *Raillietina torquata* | | | + | | | | | |
| *Raillietina* sp. | | + | | + | + | + | | |
| *Retinometra serrata* | + | | | | | | | |
| *Rostelugnia bhaulensis*† | | | + | | | | | |
| *Rostelugnia cuneata* | | | + | | | | | |
| *Rostelugnia guptai*† | | | + | | | | | |
| *Rostelugnia patialensis*† | | | + | | | | | |
| *Rostelugnia sangrurensis*† | | | + | | | | | |
| *Rostelugnia streptopeli* | + | | | | | | | |
| *Sobolevicanthus columbae* | | | + | | | | | |
| *Sobolevicanthus serratus* | + | | + | | | | | |
| *Sobolevicanthus* sp. | | + | | | | + | | |
| *Staphylepis cordobensis* | | | + | | | | | |
| *Staphylepis rustica* | | | + | | | | | |
| *Taenia crassula** | | | + | | | | | |
| *Tetrabothrioporina indica* | + | | | | | | | |
| *Valipora matolaensis* | | | + | | | | | |
| *Valipora yamaguti* | | | + | | | | | |
| Total | 12 | 6 | 63 | 2 | 3 | 4 | 0 | 0 |

* Cestode described from *Columba livia domestica* only.
† Cestode described from *Columba livia intermedia* only.
‡ Cestode described from *Columba livia domestica* and *Columba livia*.
New World sources: Mukherjee (1964); Rutherford and Black (1974); Conti and Forrester (1981); Canadian Council on Animal Care (1984); Bennett and Pierce (1990); Johnston (1992); Mueller (1992); Mirachi and Basket (1994); Gicik and Arslan (1999); Erwin et al. (2000); Glass et al. (2002); Schwertner et al. (2002); Forrester and Spalding (2003); Foronda et al. (2004); Bean et al. (2005).
Old World sources: Mukherjee (1964); Rutherford and Black (1974); Gicik and Arslan (1999); Foronda et al. (2004); and museum listings.