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# **Research Paper**

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Helminth community and host dynamics in northern bobwhites from the Rolling Plains Ecoregion, U.S.A.

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#### **Abstract**

One hundred and sixty-one northern bobwhites (Colinus virginianus; hereafter 'bobwhite') were examined from the Rolling Plains ecoregion of Texas and western Oklahoma from 2011 to 2013. Complete necropsies yielded 13 species, of which two are new host (Gongylonema phasianella) and region (Eucoleus contortus) records and three (Dispharynx nasuta, Tetrameres pattersoni and Oxyspirura petrowi) are known to cause morbidity and mortality. Of the species found, Aulonocephalus pennula commonly occurred, Oxyspirura petrowi was intermediate in prevalence, and the remaining species were rare. Species richness was similar compared to studies from the southeastern U.S., but higher than studies from the same region. In addition, 12 of the 13 species were heteroxenous helminths, supporting the theory that heteroxenous helminths in semi-arid regions are more successful than monoxenous helminths. Prevalence and abundance of A. pennula and O. petrowi were higher in adult bobwhites than in juveniles. Abundance of A. pennula and O. petrowi was higher at southern locations compared to northern locations in the study area. Our study is the first to provide a current assessment of the bobwhite helminth community across the Rolling Plains ecoregion of the U.S.

#### Introduction

The northern bobwhite (*Colinus virginianus*, hereafter bobwhite) is an upland game bird species with populations persisting in many ecologically and climatically diverse regions in the eastern half of North America. A slow, but apparent, range-wide decline in bobwhite populations has been occurring over the past 50 years (Hernández *et al.*, 2013; Sauer *et al.*, 2013; Texas Parks and Wildlife Department, 2013). Bobwhite populations fluctuate in a boom and bust pattern, where years with increased productivity are shown to be positively associated with breeding season (April–August) precipitation (Kiel, 1976; Tri *et al.*, 2013). When periods of above-average precipitation in 2010 preceded below-average bobwhite population estimates (Texas Parks and Wildlife Department, 2013), the relationship between helminths and bobwhite populations was revisited as a potential factor in the decline (Bruno, 2014; Dunham *et al.*, 2016; Villarreal *et al.*, 2016).

Much of the early research on bobwhite helminths in the Rolling Plains lacked analyses at the infra and component community levels, reporting results from incomplete necropsies focusing on particular helminth species (Webster & Addis, 1945; Jackson & Greene, 1965; Kocan *et al.*, 1979; Rollins, 1980; Boggs *et al.*, 1990), or based on studies with small geographical scale (two counties; Villarreal *et al.*, 2016), whereas research using a helminth community approach based on complete necropsies has been conducted in the Southern Coastal Plains in Florida and Georgia (Moore *et al.*, 1986; Moore & Simberloff, 1990; Davidson *et al.*, 1991). Because the Southern Coastal Plains differs ecologically and climatically (which influence helminth populations and communities) from the Rolling Plains ecoregion, host–helminth dynamics cannot be extrapolated between regions.

To learn more about diseases and potential disease agents within the Rolling Plains of Texas and Oklahoma, a large-scale bobwhite disease study, called Operation Idiopathic Decline (OID), was initiated in August 2011 in partnership with the Rolling Plains Quail Research Foundation, Texas Tech University, Texas A&M University-Kingsville, Texas A&M University, Texas A&M AgriLife Extension, and the Oklahoma Department of Wildlife and Conservation. We initiated a large-scale helminth study as part of the OID project. Our goals were to assess helminth prevalence, intensity, abundance and community structure (infra and component) in bobwhites and determine how infections are related to intrinsic (host age and host sex) and extrinsic variables (month, year of collection, and northing), thereby providing a current description of this host–helminth system at a regional scale.

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#### Materials and methods

#### Study area

Bobwhite collections predominantly occurred in the Rolling Plains ecoregion of Texas and western Oklahoma (i.e. Central Great Plains; fig. 1). The Rolling Plains is characterized by rolling rangelands dominated by honey mesquite (*Prosopis glandulosa*), Pinchot's juniper (*Juniperus pinchotii*), and prickly pear (*Opuntia* spp.) (Rollins, 2007). Annual rainfall varies from 400 mm along the westward edge to 750 mm along the east; average annual temperatures are 15–17°C across the region (Rollins, 2007; Texas Parks and Wildlife Department, 2013).

## Host collection

Bobwhites were live trapped using wire mesh funnel traps baited with grain sorghum (Sorghum bicolor) and covered with vegetation to mitigate thermal stress and aid in concealment from predators (for more detail see Bruno, 2014; Dunham et al., 2016). We trapped bobwhites for two weeks in August and October in 2011, 2012 and 2013. This sampling interval was selected to avoid the peak breeding and nesting season during spring and summer (March-July) and the hunting season in autumn and winter (November-February). We processed bobwhites within 12 h of capture. We determined age and sex according to plumage characteristics. As part of a landowner agreement under the OID project protocol, a maximum of 30 bobwhites could be captured per study site over a 3-day sample period. Computer-generated random selection was used to determine which birds went to the various projects being conducted under OID. Bobwhites designated for necropsy were euthanized using cervical dislocation, and flash frozen immediately following death. Carcasses were wrapped in aluminium foil and placed within a small Styrofoam cooler with dry ice and ethanol to rapidly cool samples and prevent autolysis of helminths (Pence et al., 1988). Bobwhite carcasses remained frozen until necropsy.

# Helminth collection, processing and identification

Frozen carcasses were thawed in a refrigerator the night before necropsy to reduce damage to parasites from repeated freezing and thawing. Complete necropsies were performed on all sample hosts (see Bruno, 2014 and Bruno et al., 2015 for a detailed description of procedures and specific helminth microhabitats examined). Nematodes were fixed in glacial acetic acid and preserved in 70% alcohol and 8% glycerin in individually marked vials corresponding to each bird and organ. Acanthocephalans and cestodes were fixed in acid-formalin-ethyl alcohol (AFA) solution and preserved in 70% alcohol in individual vials. Specimens were examined in ethyl alcohol wet mounts, identified and counted. Acanthocephalans and cestodes were stained using Mayer's Carmine Alum and mounted in Canada balsam on microscope slides. Cestodes were counted based on the number of scolices found within each cestode-infected host. Voucher specimens were deposited at the Sam Houston State University Parasite Museum, Sam Houston State University, Huntsville, SHSUP000336-381 (accession numbers SHSUP000474-483). Parasitological terms follow Bush et al. (1997). Rare species were defined as those with <25% prevalence, intermediate species with ≥25 and <75% prevalence, and common species with ≥75% prevalence across the collective host sample (Landgrebe et al., 2007).

#### Statistical analyses

Statistical analyses were conducted using the intermediate and common helminth species. A chi-square analysis using IMP<sup>®</sup> 10.0 software (SAS Institute Inc., Cary, North Carolina, USA) was used to determine if prevalence for the intermediate and common species differed by host age [adult, juvenile], host sex [male, female], month [August, October], and year of collection [2011, 2012, 2013]. Abundance data for the intermediate and common species were aggregated towards zero. To account for non-normality, data were fitted with a negative binomial distribution and regressed using a generalized linear mixed model procedure (PROC GLIMMIX) with SAS 9.2 software (SAS Institute Inc.). Models were developed to explain variation in helminth abundance of the intermediate and common species. The initial model included the main effects variables (host age, host sex, month, year of collection, and northing [Universal Trans Mercator Northing coordinate; distance north in km]), and their relevant interactions (host age\*host sex, host age\*year, and host age\*month). Backwards variable elimination was used to estimate the bestfitting model at  $P \le 0.05$  (for each included independent variable). This method allowed estimation of the relationship between the number of helminths and each variable, while accounting for effects of multicollinearity among parameters. A pseudo- $r^2$  (Nakagawa & Schielzeth, 2013) was calculated to estimate the amount of variation in helminth abundance explained by the model. Least squares means were estimated using the inverse of a log link function to compare effects among levels of categorical variables. These estimates are different from the arithmetic means reported in the descriptive analyses. Descriptive statistics are presented as mean  $\pm$  SE. Statistical tests were considered significant at  $P \le 0.05$ .

Two types of community analyses were used on the helminth data. The Percent Similarity Index (Ps<sub>i</sub>; Krebs, 1989) compared proportions of species among host component communities. Numerical similarity of helminth species was measured using Jaccard's Coefficient of Similarity Index (C<sub>i</sub>; Magurran, 1988).

## Results

From August and October 2011–2013, we collected 161 bob-whites. Of these, 13 birds were collected from three adjacent ecoregions (Edwards Plateau, High Plains, and Southwestern Tablelands) within 60 km of the Rolling Plains ecoregion boundary (fig. 1). The sample comprised 31 adult males, 21 adult females, 53 juvenile males and 56 juvenile females. By collection period, sample size was as follows: August and October 2011, 29 adults, 12 juveniles; August and October 2012, 10 adults, 46 juveniles; August and October 2013, 13 adults, 51 juveniles.

## Helminth fauna

We identified 13 species of helminths (9 nematodes, 3 acanthocephalans (1 species being a cystacanth) and 1 cestode) from 12 microhabitats representing 14,428 helminth individuals (table 1). Aulonochephalus pennula (= A. lindquisti) was the most prevalent (73%) and numerically dominant species (95% of all helminth individuals), followed by Oxyspirura petrowi (40% prevalence; 3% of all helminth individuals); the remaining species rarely

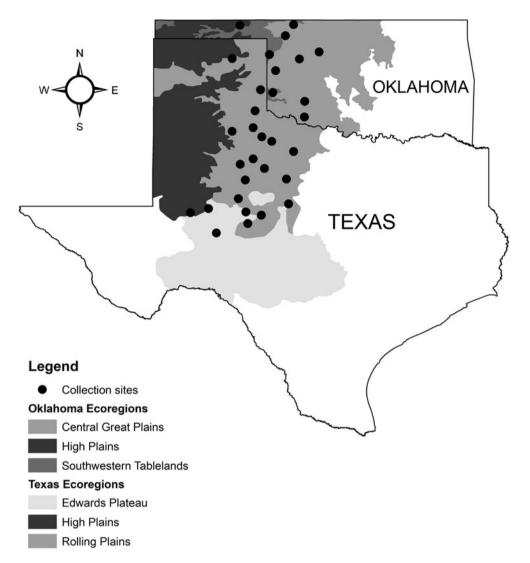


Fig. 1. Helminths were collected from northern bobwhites (*Colinus virginianus*) during August and October 2011–2013 from collection sites in the Rolling Plains ecoregion of Texas and western Oklahoma, and three adjacent ecoregions. Note: Oklahoma does not categorize its ecoregions similarly to Texas; Rolling Plains ecoregion of Texas = Central Great Plains of Oklahoma.

occurred (table 1). Intensity and abundance followed the same pattern of species numerical dominance as prevalence.

(51%) and 2013 (48%). Prevalence of *O. petrowi* was similar (P = 0.785) between 2011 and 2013.

#### Prevalence by age, sex, month and year

Prevalence and abundance were examined statistically for two species (A. pennula and O. petrowi), based on their overall prevalence of  $\geq 25\%$ . Prevalence of A. pennula in adult bobwhites (90%) was significantly higher (P=0.0005) than in juveniles (64%), but prevalence did not differ (P=0.712) between males (73%) and females (73%). Prevalence of O. petrowi was significantly greater (P=0.0001) in adult bobwhites (63%) compared to juveniles (28%), but prevalence did not differ (P=0.400) between males (43%) and females (36%). Prevalence of O. O001 than in O

# Trend analyses of parasite abundance

The best model for *A. pennula* was the following: abundance = age + northing (associated *F* and *P* values presented in table 2). The model explained 12.5% of the variation in *A. pennula* abundance (pseudo- $r^2$  = 0.125). Estimated mean of *A. pennula* in adults (161.2 ± 40.9) was significantly higher than in juveniles (43.8 ± 7.7). For any given age, an estimated slope of 0.00139 is interpreted as follows: estimated mean number of *A. pennula* decreases by 0.139% for each 1 km increase in northing.

The best model for *O. petrowi* was the following: abundance = age + sex + age\*sex + year + northing (associated*F*and*P*values presented in table 2). The model explained 31% of the variation in*O. petrowi* $abundance (pseudo-<math>r^2 = 0.31$ ). The main effect of host sex was not significant on its own, but it was included in the model because of the age\*sex interaction. The interaction effect between age\*and sex showed the estimated mean of *O. petrowi* 

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**Table 1.** Prevalence (number of infected, % infected, and 95% confidence intervals [CI]), intensity (mean ± SE; range), and abundance (mean ± SE) of helminths from 161 northern bobwhites (*Colinus virginianus*) collected during August and October 2011–2013 within the Rolling Plains ecoregion of Texas and western Oklahoma.

|                                      |     | Prevalence      | Intensity    |       | Abundance     |        |
|--------------------------------------|-----|-----------------|--------------|-------|---------------|--------|
| Helminth species <sup>a</sup>        | No. | % (95% CI)      | Mean ± SE    | Range | Mean ± SE     | Total  |
| Aulonocephalus pennula (SI, L, C)    | 117 | 73% (65.8–79.5) | 116.9 ± 11.6 | 1-617 | 84.9 ± 9.1    | 13,675 |
| Oxyspirura petrowi (E)               | 64  | 40% (32.2-47.3) | 7.7 ± 1.5    | 1-61  | $3.1 \pm 0.6$ | 495    |
| Acanthocephalan larvae (E, N, C, SI) | 15  | 9% (4.8–13.8)   | 5.3 ± 2.1    | 1-32  | 0.5 ± 0.2     | 80     |
| Tetrameres pattersoni (P)            | 23  | 14% (8.8–19.7)  | 3.0 ± 0.5    | 1-10  | $0.4 \pm 0.1$ | 69     |
| Physaloptera sp. (BM)                | 11  | 7% (2.9–10.7)   | 4.1 ± 1.1    | 1–12  | $0.3 \pm 0.1$ | 45     |
| Rhabdometra odiosa (SI)              | 12  | 7% (4.8–13.8)   | 3.7 ± 1.0    | 1–12  | 0.3 ± 0.1     | 44     |
| Gongylonema phasaniella (C)          | 3   | 2% (<0.1-3.9)   | 3.3 ± 0.3    | 1-4   | 0.1 ± < 0.1   | 10     |
| Cheliospirura spinosa (G)            | 2   | 1% (<0.1-2.9)   | 1.5 ± 0.5    | 1–2   | <0.1 ± <0.1   | 3      |
| Dispharynx nasuta (P)                | 2   | 1% (<0.1-3.9)   | 1.0 ± 0.0    | 1     | <0.1 ± <0.1   | 2      |
| Mediorhynchus papillosus (SI)        | 2   | 1% (<0.1-2.9)   | 1.0 ± 0.0    | 1     | <0.1 ± <0.1   | 2      |
| Eucoleus contortus (C)               | 1   | 1% (N/A)        | 1.0 ± N/A    | 1     | <0.1 ± <0.1   | 1      |
| Mediorhynchus sp. (SI)               | 1   | 1% (N/A)        | 1.0 ± N/A    | 1     | <0.1 ± <0.1   | 1      |
| Subulura brumpti (C)                 | 1   | 1% (N/A)        | 1.0 ± N/A    | 1     | <0.1 ± <0.1   | 1      |

<sup>&</sup>lt;sup>a</sup> Microhabitats: BM, breast muscle; C, ceca; E, eye surface, nictitating membrane, associated glands, and ducts; G, gizzard; L, large intestine; N, neck muscle; P, proventriculus; SI, small intestine

**Table 2.** F and P values generated from the final main and interaction effects variables of the negative binomial generalized linear regression model for Aulonocephalus pennula and Oxyspirura petrowi from 161 northern bobwhites (Colinus virginianus) collected during August and October 2011–2013 within the Rolling Plains ecoregion of Texas and western Oklahoma.

| Aulonocephalus pennula  |       |         |                         | Oxyspirura petrowi |         |  |
|-------------------------|-------|---------|-------------------------|--------------------|---------|--|
| Effect                  | F     | Р       | Effect                  | F                  | Р       |  |
| Age                     | 17.75 | <0.0001 | Age                     | 32.41              | <0.0001 |  |
| Northing                | 4.61  | 0.0334  | Year                    | 6.18               | 0.0026  |  |
| Age * Sex <sup>a</sup>  | 1.54  | 0.2165  | Northing                | 21.04              | <0.0001 |  |
| Age * Year <sup>a</sup> | 0.73  | 0.4852  | Age * Sex               | 5.51               | 0.0049  |  |
|                         |       |         | Age * Year <sup>a</sup> | 0.23               | 0.7954  |  |

<sup>&</sup>lt;sup>a</sup>Non-significant interaction terms retained in final model when it included a significant main effects variable.

in adult males  $(11.0\pm3.7)$  was significantly higher than in adult females  $(1.8\pm0.8)$ , juvenile males  $(0.4\pm0.2)$ , and juvenile females  $(0.6\pm0.2)$ . The estimated mean of *O. petrowi* by year was similar between 2011  $(1.7\pm0.5)$  and 2013  $(3.2\pm0.9)$ , and similar between 2011 and 2012  $(0.7\pm0.2)$ , but was significantly higher in 2013 compared to 2012. For any given age\*sex combination in each year, an estimated slope of -0.00376 is interpreted as follows: estimated mean number of *O. petrowi* decreases by 0.376% for each 1 km increase in northing. Although there is a large amount of variation in abundance not explained by the variables included in regression models (low  $r^2$  values), the significant variables in these models can still be used to draw important conclusions about helminth abundance in this sample (see Discussion).

## Helminth community dynamics

Infracommunity species richness ranged from 1 to 5, with 1 to 2 species occurring in a majority (64%) of the hosts. Species distribution by year showed a similar pattern among hosts, with 1 to 2 occurring in a majority of the hosts for each year (fig. 2). There

was only one year (2012) in which host individuals (n = 9) had more than four helminth species.

Based on  $PS_i$  values, component communities were almost completely similar among host age, host sex, month and year (table 3). Component communities within each comparison were numerically dominated by *A. pennula*, accounting for 90 to 98% of all helminth individuals. *Oxyspirura petrowi* accounted for 2 to 7% of the total individuals for each comparison, and all other species accounted for < 1%.

Jaccard's Coefficient of Similarity (C<sub>j</sub>) found seven (54%) shared species between adults (10 helminth species) and juveniles (10 species), and seven (54%) shared species between male (11 species) and female (9 species) host helminth communities (table 3). The host helminth community in August (11 species) and October (11 species) shared nine (70%) of the species that occurred in each month. Component communities between 2011 (7 species) and 2012 (10 species) shared six (50%) of the species found in each year. Component communities between 2011 and 2013 (9 species) were slightly less similar, sharing five (45%) of the species found in each year. Component communities

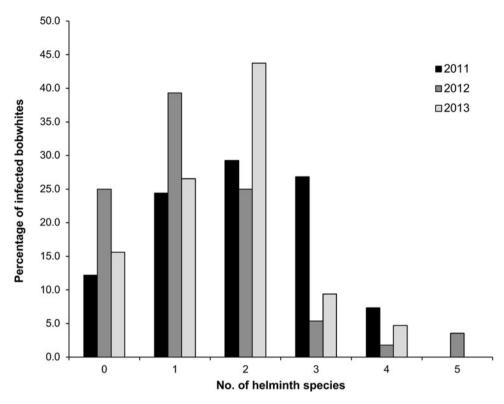


Fig. 2. Distribution of helminth species by year in 161 northern bobwhites (Colinus virginianus) collected during August and October 2011 (black bars), 2012 (grey bars) and 2013 (white bars) within the Rolling Plains ecoregion of Texas and western Oklahoma.

**Table 3.** Comparisons of Percent Similarity ( $PS_i$ ) and Jaccard's Coefficient of Similarity ( $C_j$ ) indices for helminth communities by host age, host sex, month and year from 161 northern bobwhites (*Colinus virginianus*) collected during August and October 2011–2013 within the Rolling Plains ecoregion of Texas and western Oklahoma.

| Comparison   | PS <sub>i</sub> | Cjb  |
|--|-----------------|------|
| Adults ( <i>n</i> = 52) vs Juveniles ( <i>n</i> = 109) | 96.8            | 0.54 |
| Males (n = 84) vs Females (n = 77)                     | 96.4            | 0.54 |
| August $(n = 84)$ vs October $(n = 77)$                | 98.3            | 0.70 |
| 2011 (n = 41) vs 2012 (n = 56)                         | 98.0            | 0.50 |
| 2011 (n = 41) vs 2013 (n = 64)                         | 98.2            | 0.45 |
| 2012 (n = 56) vs 2013 (n = 64)                         | 99.1            | 0.67 |

 $<sup>^{\</sup>rm a}$  Values for PS, range from 0 to 100, where 0=completely dissimilar communities, and 100=completely similar communities.

between 2012 and 2013 were more similar than comparisons between other years, sharing eight (67%) species found in each year (table 3). In each comparison, the helminths not shared by both component communities represent rare species and occurred in <2% of the population.

# **Discussion**

## Helminth community dynamics

The helminth component community was composed largely of heteroxenous species (12 of 13 species), but was numerically

dominated by a single species (A. pennula). Helminth species richness values in the present study are similar to those found in the southeastern U.S., but higher than in other bobwhite studies from Texas (Parmalee, 1952; Purvis et al., 1998; Villarreal et al., 2016). Cram et al. (1931) reported 12 species of helminths in wild bobwhites throughout the eastern U.S., and several surveys from Florida reported 12-15 species of helminths (Davidson et al., 1980, 1991; Moore et al., 1986; Moore & Simberloff, 1990). These component communities consisted of a similar distribution of intermediate and rare species to our study, but they had higher occurrences of common species (n = 3). Species composition also differed between the component communities in the southeastern U.S. and our study. Aulonocephalus pennula was the numerically dominant species in our study and is a common (>75% prevalence) and abundant species found in quail species from Texas (Webster & Addis, 1945; Lehmann, 1984; Landgrebe et al., 2007; Bedford, 2015; Olsen & Fedynich, 2016; Villarreal et al., 2016) and New Mexico (Campbell & Lee, 1953), but is not found in bobwhites from Florida, Georgia (Kellogg & Prestwood, 1968), North Carolina (Cram et al., 1931; Blakeney & Dimmick, 1971) or Kansas (Williams et al., 2004). Component communities in the southeastern U.S. also consist of more monoxenous nematode species (range: 2-4), which occurred in high intensities (>30; Moore et al., 1986; Moore & Simberloff, 1990; Davidson et al., 1991). The difference in species composition and variation in life cycles of helminths across the bobwhite's geographical range is probably the result of mesic conditions found in the southeastern U.S., compared to the more semi-arid Rolling Plains.

It has been suggested that the dominance of heteroxenous species within a helminth community in semi-arid to arid regions

 $<sup>^{\</sup>rm b}$  Values for  $C_{\rm j}$  range from 0 to 1, where 0=completely dissimilar communities, and 1=completely similar communities.

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may be a survival strategy (Fedynich et al., 2001; Landgrebe et al., 2007). Helminths can persist longer in harsher environments if they maintain infective stages in intermediate hosts (Mackiewicz, 1988). This may be why direct life cycle helminths such as Heterakis spp., Trichostrongylus tenuis, Strongyloides spp. and Capillaria spp. are more common in bobwhites from mesic areas in the southeastern U.S. (Cram et al., 1931; Kellogg & Prestwood, 1968; Davidson et al., 1980, 1991; Moore et al., 1987; Moore & Simberloff, 1990). This is supported by studies that have found a high prevalence of T. tenuis in bobwhites from Texas (Demarais et al., 1987; Purvis et al., 1998), where study areas were dominated by poorly drained clay soils which received precipitation that exceeded the long-term average for the Rolling Plains. Similarly, high intensities of Heterakis gallinae were found in bobwhites from north-eastern Texas, a forested region where precipitation and humidity are relatively higher than other areas of Texas (Parmalee, 1952).

## Factors influencing helminth population dynamics

Host age was an important variable for both *A. pennula* and *O. petrowi* populations, with more adults infected and having a higher intensity of infection than juveniles. An age effect has been found for various helminth species in bobwhites (Davidson *et al.*, 1980; Forrester *et al.*, 1984; Moore *et al.*, 1986; Davidson *et al.*, 1991; Dunham *et al.*, 2014, 2016; Villarreal *et al.*, 2016). Host age-related differences are attributed to time-related accumulation in adults resulting from longer exposures to infective stages of helminths (Davidson *et al.*, 1980).

Host sex alone was not an important variable in *A. pennula* and *O. petrowi* prevalence or abundance. Host sex is usually not a significant variable in parasite infections of bobwhites (Blakeney & Dimmick, 1971; Moore *et al.*, 1987). Similarities in male and female social behaviour and diet probably create equal exposure probabilities to helminth infective stages. Higher numbers of *O. petrowi* were found in adult males compared to any other age\*sex combination. The biological significance of this interaction is unknown. We would expect this result in adult females because of their higher protein (mainly sourced from arthropods) requirements during reproduction (Hernández & Peterson, 2007), as found by Dunham *et al.* (2014).

Concerns have been raised regarding negative impacts of A. pennula on bobwhites (Dunham et al., 2017). Similar to Olsen & Fedynich (2016), we observed distension in the terminal portions of the ceca when A. pennula infections were high (>300 worms). Nematodes may take advantage of regulatory molecules to evade the host immune system (Maizels et al., 2001), creating tolerance and allowing infections to persist. This phenomenon has not been investigated for the helminths occurring in bobwhites, but it may be possible that the success of A. pennula in bobwhites is because of immunomodulators. Consistent with previous descriptions (Chandler, 1935), we did not find A. pennula attached to the cecal wall, and Dunham et al. (2017) observed no inflammation or lesions in bobwhites with high infections. It is possible that intensities of A. pennula in bobwhites are high because an antibody response is not occurring as a result of noninvasive contact with host tissues.

The only significant difference detected by month was prevalence of *A. pennula*, increasing from August to October. Villarreal *et al.* (2016) found a similar seasonal effect, where the prevalence of *A. pennula* increased from the summer to early winter period. *Oxyspirura petrowi* prevalence and abundance in our

study was lowest in 2012, but similar between 2011 and 2013. One explanation is that 82% of the bobwhites sampled in 2012 were juvenile birds and only six individuals were infected with *O. petrowi*.

Counts of both *A. pennula* and *O. petrowi* were found to increase in the study area from north to south. Jackson & Green (1965) similarly noted that *O. petrowi* prevalence was higher in their southern collection sites in the Rolling Plains compared to their northern sites. This spatial pattern could be affected by the variation of bobwhite density, distribution of the insect intermediate hosts (Keymar & Anderson, 1979), precipitation and habitat across the study area.

Our study documented bobwhite helminth community composition at a regional scale in a landscape where bobwhites are highly valued both ecologically and economically. The prevalence and spatial patterns of O. petrowi in bobwhites found in earlier studies (Jackson & Green, 1965) were similar to our study, reflecting relatively average stable trends for this species when sampled across the entire ecoregion. We also confirm recent documentations of high prevalence, intensity and abundance of A. pennula (Villarreal et al., 2016; Dunham et al., 2017). Current research focusing on understanding the life cycles of A. pennula and O. petrowi (Kistler et al., 2016; Henry et al., in press) may help clarify their patterns of numerical dominance in the region. Additionally, continued study of the bobwhite-helminth system will provide insight into the infection dynamics of helminths currently reported within the Rolling Plains ecoregion and aid in monitoring current pathogenic helminths (i.e. O. petrowi, Dispharynx nasuta and Tetrameres pattersoni) and the possible establishment of additional helminth species within the region.

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Conflict of interest. None.

**Ethical standards.** Bobwhites were collected in accordance with established permits and protocols approved by the TAMUK Institutional Animal Care and Use Committee (2009-09-21A), TAMU (AUP 2011-193), TAMUK Institutional Biosafety Committee (IBC-ID#009-2011), and Texas Parks and Wildlife Department Scientific Research permit (SPR-0690-152).

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