

EXPLORING A PLANT-DIVERSITY HYPOTHESIS TO EXPLAIN HELMINTH PREVALENCE IN NORTHERN BOBWHITE (*COLINUS VIRGINIANUS*) IN TEXAS, USA

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ABSTRACT: Helminths, in particular eyeworms (*Oxyspirura petrowi*) and cecal worms (*Aulonocephalus pennula*), may be a factor influencing northern bobwhite (*Colinus virginianus*) populations in Texas. Previous research has shown a discrepancy in helminth infections between the Rolling Plains and Rio Grande Plains of Texas, US, potentially caused by differences in intermediate host distribution and abundance. We explored an alternative hypothesis centered on plant diversity, given that many plants possess phytochemicals with anthelmintic properties. We predicted that plant diversity would be greater and bobwhite diet more diverse in the Rio Grande Plains than the Rolling Plains, which in turn would potentially expose bobwhites to more plants with anthelmintic properties and therefore result in lower parasite prevalence and intensity. We conducted a literature review of plant diversity, anthelmintic plants, and bobwhite diet in Texas to explore this hypothesis. We also quantified the relationship between helminth prevalence in bobwhites and latitude. We documented trends for higher plant species richness, greater number of anthelmintic plants, and more diverse bobwhite diet in the Rio Grande Plains compared to the Rolling Plains. In addition, we documented a trend for increasing helminth prevalence with latitude for eyeworms but not cecal worms. Our study provides circumstantial evidence supporting the plant-diversity hypothesis and warrants experimental testing.

Key words: Anthelmintic plants, *Aulonocephalus pennula*, cecal worms, eyeworms, northern bobwhite, *Oxyspirura petrowi*, nutritional wisdom, plant diversity, self-medication.

INTRODUCTION

The Northern Bobwhite (*Colinus virginianus*) has been experiencing a population decline across its geographic distribution. Bobwhites, a species of quail, are a popular gamebird that inhabit savannahs, grasslands, and shrublands and eat a diverse diet of seeds, mast, plant material, and arthropods. Habitat loss and fragmentation are considered ultimate causes of the bobwhite decline with local factors (e.g., predators, fire ants, nonnative invasive grasses, etc.) considered as proximate causes (Brennan 1991; Hernández et al. 2013). In the Rolling Plains of Texas, US, bobwhites have experienced population declines despite apparently large amounts of available habitat (Hernández 2021), and parasitism has been proposed as a proximate cause (Henry et al. 2017).

Prior to the 1980s, studies of bobwhite parasites were few, given that parasites generally were not considered to exert a major influence on quail populations (Lehmann 1984; Peterson 2007). Within the past decade, however, research on bobwhite diseases and parasites has increased tremendously, and bobwhites have been documented to harbor high intensities of two helminths: cecal worms (*Aulonocephalus pennula*) and eyeworms (*Oxyspirura petrowi*; e.g., Dunham et al. 2014; Bruno et al. 2018; Peterson and Fedynich in press). Eyeworms have been identified as a factor potentially influencing bobwhite populations in the Rolling Plains (Dunham et al. 2016). Bruno et al. (2015) discovered pathological effects of eyeworms on the cornea of bobwhites. Dunham et al. (2014) reported that bobwhites suffered from lacrimal duct inflammation with distinct petechial hemorrhaging

when eyeworm infection intensity was as low as 10–30 individuals. They also suggested that eyeworm infection may result in impaired respiratory function, visual obstruction, and decreased ability to escape predators. Jackson (1969) noted that infected quail were hesitant to fly and instead attempted to escape via running. In addition, anecdotal accounts of eyeworm-infected bobwhites flying into buildings and other anthropogenic structures have been reported (Brym et al. 2018). Although cecal worms occur in high prevalences and intensities in bobwhites from Texas, only gross pathological damage has been documented. For example, Olsen and Fedynich (2016) noted distended ceca when *A. pennula* infections were >300 worms per bobwhite. Dunham et al. (2017) also noted very little digesta in the ceca when cecal worm numbers were high (range 97–341).

There appear to be latitudinal differences in helminth prevalence and intensity in bobwhites in Texas (Olsen and Fedynich 2016; Kubečka et al. 2017, Bruno et al. 2018). Eyeworm prevalence in bobwhites has been documented to range from 40% (64/161; Bruno et al. 2018) to 86% (31/36; Dunham et al. 2014) in the northern part of the state (Rolling Plains), whereas prevalence has ranged from 4% (14/356; Shea et al. 2021) to 9% (22/244; Olsen and Fedynich 2016) in the southern part (Rio Grande Plains). Similarly, intensity of eyeworm infections has been reported at 7.7 ± 1.5 worms (mean \pm standard error, SE, Bruno et al. 2018) and 14.2 ± 0.2 in the Rolling Plains (Bruno et al. 2019) but only 1.2 ± 0.1 (Shea et al. 2021) and 4.9 ± 1.7 in the Rio Grande Plains (Olsen and Fedynich 2016). Regarding cecal worms, the latitudinal difference is not as pronounced in terms of prevalence, with studies reporting 73% (117/161; Bruno et al. 2018), 82% (117/142; Villarreal et al. 2016), and 91% (117/128; Bruno et al. 2019) in the Rolling Plains compared to 78% (162/209; Olsen and Fedynich 2016) and 81% (287/356; Shea et al. 2021) in the Rio Grande Plains. However, higher cecal worm intensities of 116.9 ± 11.6 worms (Bruno et al. 2018), 134.3 ± 11.2 (Villarreal et al. 2016),

and 140.7 ± 1.5 (Bruno et al. 2019) have been documented in the Rolling Plains compared to 48.6 ± 5.2 (Shea et al. 2021) and 82.2 ± 7.1 (Olsen and Fedynich 2016) in the Rio Grande Plains.

Keymar and Anderson (1979) hypothesized that latitudinal differences in parasite prevalence could be related to the distribution of intermediate hosts. Kistler et al. (2016) reported that the Plains Lubber Grasshopper (*Brachystola magna*) could serve as an intermediate host for eyeworms for bobwhites. Almas et al. (2018) reported *O. petrowi* DNA in six different species of grasshoppers, Texas field crickets (*Gryllus texensis*), and in wood cockroaches (*Parcoblatta* spp.). For cecal worms, Henry et al. (2018) reported that 9 of 35 species collected from the Order Orthoptera showed amplification for *A. pennula* DNA. Thus, it has been suggested that the higher helminth prevalence and intensities in the Rolling Plains might be due to differences in intermediate host distribution and abundance between ecoregions (Olsen and Fedynich 2016; Bruno et al. 2019).

We explored an alternate hypothesis, one based on plant diversity. Plant diversity tends to increase from poles to the equator, a phenomenon referred to as the latitudinal biodiversity gradient (Rohde 1992). Plants contain phytochemicals (secondary compounds), some of which possess anthelmintic properties that kill and expel parasitic worms without harming the host (Holden-Dye and Walker 2014; Provenza 2018). Animals possessing parasites have been found to self-medicate by consuming certain vegetation (de Roode et al. 2013; Morogh-Bernard et al. 2017), a process whereby animals consume natural materials to reduce or eliminate deleterious parasites or pathogens (Clayton and Wolfe 1993; Engel 2002). If greater plant species richness in the Rio Grande Plains resulted in a wider array of plants with anthelmintic properties and a broader breadth in bobwhite diet, then differences in plant diversity between the Rolling Plains and Rio Grande Plains might help explain the latitudinal difference in helminth prevalence in bobwhites.

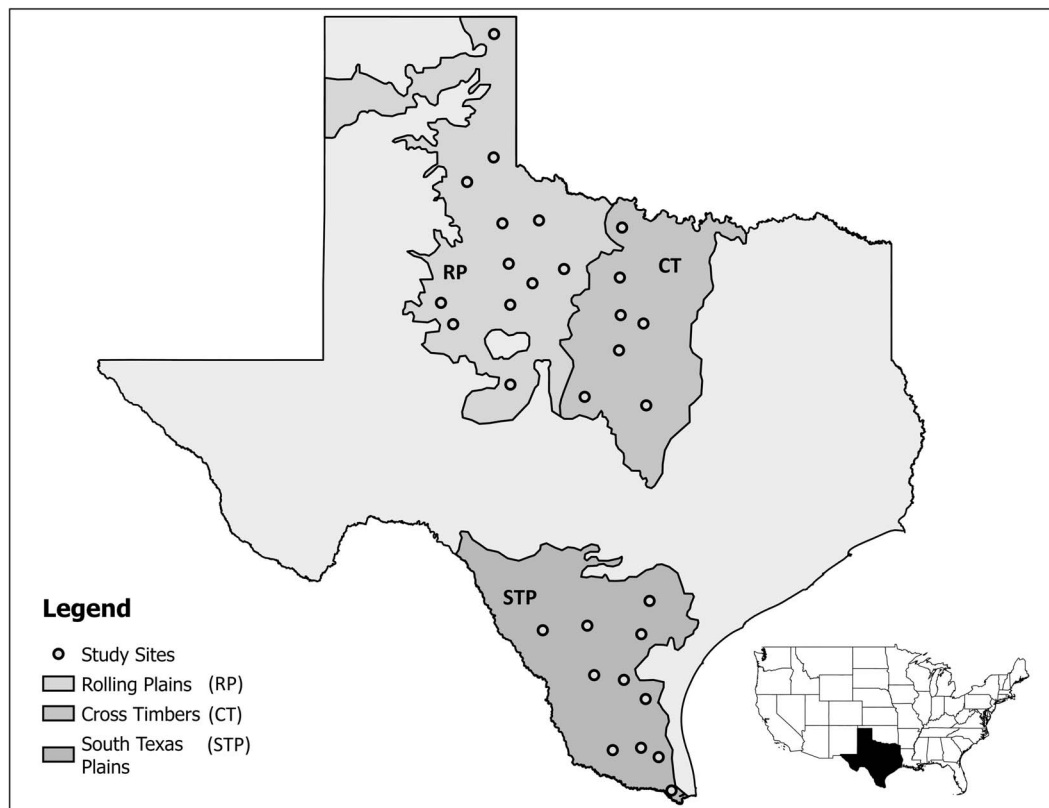


FIGURE 1. Locations of study areas and of sampling sites reported in studies documenting cecal and eyeworm prevalence in northern bobwhite (*Colinus virginianus*), in northern (Rolling Plains and Cross Timbers and Prairies) and southern (Rio Grande Plains) areas of Texas, USA, 1980–2020.

Therefore, we hypothesized that there would be greater plant species richness and anthelmintic-plant richness, as well as a broader diet breadth of bobwhites, in the Rio Grande Plains relative to the Rolling Plains.

To explore this plant-diversity hypothesis, our research objectives were to compare 1) plant species richness (number of species); 2) anthelmintic-plant richness; and 3) bobwhite diet breadth between the Rio Grande Plains and Rolling Plains ecoregions. We also wanted to formally quantify the spatial relationship between latitude and cecal worm and eyeworm prevalence in bobwhites in Texas.

MATERIALS AND METHODS

Our study focused on the Rolling Plains and Rio Grande Plains of Texas because of the large amount of research that has been conducted recently on

bobwhite parasites in these ecoregions (Fig. 1). Both ecoregions provide relatively large amounts of habitat and support significant bobwhite populations (Ritzell et al. 2022). The Rolling Plains is an extension of the Great Plains and consists of approximately 9.7 million ha of gently rolling to moderately rough terrain in northern Texas (Scifres 1980). Approximately two-thirds of the ecoregion consists of rangeland, with cow-calf operations as the common livestock enterprise (Correll and Johnston 1979). Mean annual precipitation ranges from 558 to 762 mm, with temperatures ranging from mean monthly minimum of -2.0 C in January to mean monthly maximum of 35.4 C in July (1895–2019; National Climatic Data Center 2021). The Rio Grande Plains encompasses approximately 8.1 million ha and is characterized by flat to undulating topography with elevations of 0–305 m (Gould 1975). The climate is classified as semiarid, subtropical with mean annual precipitation of 500–750 mm (Norwine and John 2007) and

temperatures ranging from mean monthly minimum of 6.1 C in January to mean monthly maximum of 36.2 C in July (1895–2019; National Climatic Data Center 2021).

We conducted three literature reviews focused on our targeted study areas in Texas to gather the necessary data to evaluate the plant-diversity hypothesis. These literature reviews consisted of searches for 1) plant species richness and plants with potential anthelmintic properties, 2) bobwhite diet, and 3) cecal worm and eyeworm prevalence in bobwhites. To document plant species richness in the study areas, we obtained distributional data of flora from the North American Plant Atlas of the Biota of North America Program (Kartez and the Biota of North America Program 2015). This atlas represents the first comprehensive attempt to provide state- and county-level distribution maps of all vascular plant taxa found within North America. We obtained density-gradient (number of species/10,000 km²) maps for native grasses and woody-plant species to assess the spatial distribution of plant species richness in Texas. We chose these two functional plant groups from the available density-gradient maps because grass seeds and woody-plant mast represent important components of the bobwhite diet (Larson et al. 2010). Forbs also represent a component of the bobwhite diet; however, the North American Plant Atlas currently does not provide a density-gradient map for forbs. We used these data to provide general estimates of plant species richness of native grasses and woody plants in the Rio Grande Plains and Rolling Plains.

We were unable to find a definitive reference book, website, or other publication for plants with anthelmintic properties. We conducted a literature search for plants with anthelmintic or medicinal properties. Search engine key phrases included “medicinal plants of North America,” “anthelmintic plant species,” “native American medicinal plants,” and “anthelmintic treatment of livestock.” Notable search engines used included ProQuest, JSTOR, ScienceDirect, Research Gate, and Google Scholar. For each plant species found during the literature search, we first determined if the plant was found in Texas and specifically in the Rolling Plains and Rio Grande Plains, using the North American Plant Atlas of the Biota of North America Program. Species not found in Texas were evaluated for close family relatives (species within the same genus) that may be found in Texas and may also possess

anthelmintic properties. Plants fitting both criteria were recorded with common and scientific names and the ecoregion(s) in which they occurred. We used these data to create a list of plants within our study areas potentially possessing anthelmintic properties.

We also conducted a literature review of bobwhite diet studies in Texas, limited to those conducted in the Rolling Plains and the Rio Grande Plains. Key search phrases used included “bobwhite crop analysis,” “bobwhite diet study,” and “quail crop study.” Because we were interested in plant species found in the bobwhite diet, our review was limited to studies that listed the plant species found in the bobwhite diet. We recorded the common and scientific name of each plant found in the bobwhite diet and the ecoregion(s) in which the plant was found, cross-referencing the species with the anthelmintic plant list.

Our final literature review included studies reporting cecal worm and eyeworm prevalence in bobwhites in Texas. Our search involved key phrases such as “parasites of bobwhites,” “quail parasites,” “cecal worms,” and “eyeworms.” For each relevant article, we noted the reported parasite prevalence (i.e., percent of individuals infected with either cecal worms or eyeworms) and obtained latitude based on the centroid of the county in which the study occurred. We conducted Mann-Whitney *U*-tests to compare mean prevalence of cecal worms and eyeworms between ecoregions. We also conducted simple linear regression to quantify the relationship between cecal and eyeworm prevalence in bobwhites and latitude. We determined the existence of a latitudinal gradient by the sign of the slope and set the level of significance at $\alpha=0.05$. We used R software for all statistical analyses (R Core Team 2022).

RESULTS

Plant species richness in Texas tended to increase from north to south, in accordance with the latitudinal biodiversity gradient. Native-grass species richness tended to be lower in the Rolling Plains (about 80–130 species/10,000 km²) than the Rio Grande Plains (about 110–160 species/10,000 km²; Supplementary Material Fig. S1A). Woody-plant species richness also tended to be lower in the Rolling Plains (about 100–175 species/10,000 km²) compared to the Rio Grande

Plains (about 200–275 species/10,000 km²; Supplementary Material Fig. S1B).

Our literature review documented a total of 118 plants in North America that potentially possessed anthelmintic properties (Table 1). Of this total, the Rio Grande Plains contained more of the potential anthelmintic plants (96/118 species; 81%) than did the Rolling Plains (72/118 species; 61%; Fig. 2A). In cross-referencing these plants with the bobwhite diet, we found that 23 plants with possible anthelmintic properties had been documented in the bobwhite diet in the Rio Grande Plains, whereas only 17 such plants had been documented in the bobwhite diet in the Rolling Plains (Fig. 2B). In addition, the breadth of the bobwhite diet was much broader in the Rio Grande Plains (99 plant species) than in the Rolling Plains (45 plant species; Fig. 2C).

Regarding helminth prevalence, mean cecal worm prevalence in bobwhites was similar between the Rio Grande Plains (74.8±12.7%; data from five sites) and the Rolling Plains (79.8±4.1%; data from 19 sites; $P=0.80$). Similarly, we did not observe a linear relationship between latitude and prevalence of cecal worms ($\beta=-1.04$; $P=0.51$; Fig. 3A). However, mean eyeworm prevalence in bobwhite was lower in the Rio Grande Plains (20.5±10.7%; data from four sites) than in the Rolling Plains (55.1±5.0%; data from 20 sites; $P=0.02$). In addition, we documented a positive (albeit still insignificant) linear relationship between latitude and prevalence of eyeworm prevalence ($\beta=3.11$; $P=0.14$; Fig. 3B).

DISCUSSION

Collectively, our findings supported our research hypotheses. We documented greater plant species richness, greater number of plants with potential anthelmintic properties, and broader breadth of the bobwhite diet in the Rio Grande Plains relative to the Rolling Plains. We also documented evidence for a latitudinal gradient in eyeworm prevalence in bobwhites in Texas, but not for cecal worm prevalence.

Plant species with anthelmintic properties provide an important source of self-medication for wild animals. Consequently, greater plant diversity creates a higher potential for an organism to encounter plant species containing anthelmintic properties. The higher plant species richness and broader diet breadth of bobwhite in the Rio Grande Plains may be increasing their likelihood of ingesting plants with anthelmintic properties in the Rio Grande Plains than the Rolling Plains. Although such a process would be passive rather than intentional, self-medication has been documented in a variety of domestic and wild animals (Villalba et al. 2014). For example, Hutchings et al. (2003) documented that parasitized mammals were “aware” of their parasitic state, thereby allowing for selection and consumption of plants containing antiparasitic compounds (i.e., self-medication). By consuming a diversity of plants, parasitized mammals were able to benefit from the anthelmintic properties of plants. Masello et al. (2018) also reported that parrots (Psittaciformes) from the Indo-Malayan, Australasian, and Neotropical zoogeographical regions were capable of self-medication, consuming plants that were known for their secondary metabolites. Self-medicating parrots were documented to be free of hemoparasites, whereas those that did not remained parasitized. However, it is unknown whether self-medication occurs in bobwhites.

Similar to our observation of differences in plant species richness and diet breadth between ecoregions, we also documented varying parasite prevalence in bobwhites in relation to latitude. Interestingly, we documented a positive trend in prevalence with latitude for eyeworms but not for cecal worms. These contrasting relationships may result from differences in the microhabitats inhabited by these two types of helminths in the bobwhite host. Eyeworm larvae are found within infected intermediate hosts (e.g., grasshoppers) that are temporarily stored in the crop when consumed by a bobwhite (Kalyanasundaram 2019). Eyeworm larvae then make their way through the esophagus,

TABLE 1. Plant species potentially possessing anthelmintic properties, Rio Grande Plains and Rolling Plains, Texas, US. List developed based on a literature search for medicinal and anthelmintic plants in North America.

Scientific name	Common name	Rio Grande Plains	Rolling Plains	Bobwhite diet	Source
<i>Acacia rigidula</i>	Blackbrush	X		Y	McBride et al. (2020)
<i>Achillea millefolium</i>	Common yarrow	X	X		Borchers et al. (2000)
<i>Adiantum capillus-veneris</i>	Maidenhair fern	X	X		Foster and Duke (2000)
<i>Amaranthus palmeri</i>	Carelessweed	X	X	Y	Foster and Duke (2000)
<i>Ambrosia psilostachya</i>	Common ragweed	X	X	Y	McBride et al. (2020)
<i>Amyris texana</i>	Texas torchwood	X			McBride et al. (2020)
<i>Anemopsis californica</i>	Lizard tail		X		McBride et al. (2020)
<i>Argemone albiflora</i>	White pricklypoppy	X			Foster and Duke (2000)
<i>Argemone mexicana</i>	Mexican prickly poppy	X			McBride et al. (2020)
<i>Argemone sanguinea</i>	Red pricklypoppy	X		Y	Foster and Duke (2000)
<i>Artemisia dracunculoides</i>	Tarragon		X		McBride et al. (2020)
<i>Artemisia ludoviciana</i>	White sagebrush	X	X		McBride et al. (2020)
<i>Artemisia mexicana</i>	Cudweed sawewort	X			McBride et al. (2020)
<i>Arundo donax</i>	Giant reed	X	X		McBride et al. (2020)
<i>Avena sativa</i>	Common oat	X	X		McBride et al. (2020)
<i>Bassia scoparia</i>	Kochia		X	Y	Rajeswari (2014)
<i>Borago officinalis</i>	Borage	X	X		Foster and Duke (2000)
<i>Bouteloua eriopoda</i>	Black grama		X	Y	McBride et al. (2020)
<i>Brassica nigra</i>	Black mustard	X	X		Foster and Duke (2000)
<i>Brassica oleracea</i>	Wild cabbage	X	X		McBride et al. (2020)
<i>Brassica rapa</i>	Field mustard	X	X		Foster and Duke (2000)
<i>Callicarpa americana</i>	American beautyberry	X			Setzer (2018)
<i>Capsella bursa-pastoris</i>	Shepherd's purse	X	X		Foster and Duke (2000)
<i>Capsicum annuum</i>	Sweet pepper	X			McBride et al. (2020)
<i>Castela erecta</i>	Allthorn goatbush	X			McBride et al. (2020)
<i>Cichorium intybus</i>	Common chicory	X	X		Setzer (2018)
<i>Cirsium arvense</i>	Creeping thistle	X	X	Y	Foster and Duke (2000)
<i>Commelina communis</i>	Dayflower	X	X	Y	Foster and Duke (2000)
<i>Commelina erecta</i>	Whitemouth dayflower	X	X	Y	Foster and Duke (2000)
<i>Convolvulaceae</i>	Blindweed	X		Y	McBride et al. (2020)
<i>Croton capitatus</i>	Hogwort	X		Y	McBride et al. (2020)
<i>Croton glandulosus</i>	Vente conmigo	X	X	Y	McBride et al. (2020)
<i>Croton monanthogynus</i>	Prarie tea	X	X		McBride et al. (2020)
<i>Croton texensis</i>	Texas croton	X	X	Y	McBride et al. (2020)
<i>Croton punctatus</i>	Gulf croton	X		Y	McBride et al. (2020)
<i>Cucurbita foetidissima</i>	Stinking gourd		X		McBride et al. (2020)
<i>Cynodon dactylon</i>	Bermuda grass	X	X		McBride et al. (2020)
<i>Datura wrightii</i>	Jimsonweed	X			McBride et al. (2020)
<i>Descurainia pinnata</i>	Western tansymustard	X	X	Y	McBride et al. (2020)
<i>Desmodium tweedyi</i>	Tweedys tickflower		X		Foster and Duke (2000)
<i>Diospyros texana</i>	Common persimmon	X	X	Y	Foster and Duke (2000)
<i>Distichlis spicata</i>	Saltgrass	X	X		McBride et al. (2020)
<i>Equisetum laevigatum</i>	Smooth horsetail		X		Setzer (2018)
<i>Ericameria laricifolia</i>	Turpentine bush	X	X		McBride et al. (2020)
<i>Ericameria nauseosa</i>	Rubber rabbitbrush	X	X		McBride et al. (2020)
<i>Erigeron canadensis</i>	Horseweed	X	X		Setzer (2018)
<i>Eryngium leavenworthii</i>	Leavenworth's eryngo		X		Setzer (2018)
<i>Eupatorium perfoliatum</i>	Boneset	X	X		Setzer (2018)

TABLE 1. Continued.

Scientific name	Common name	Rio Grande Plains	Rolling Plains	Bobwhite diet	Source
<i>Euphorbia albomarginata</i>	Rattlesnake sandmat	X	X	Y	McBride et al. (2020)
<i>Euphorbia antisyphilitica</i>	Candelilla	X		Y	McBride et al. (2020)
<i>Euphorbia fendleri</i>	Fendlers sandmat	X		Y	Foster and Duke (2000)
<i>Forestiera pubescens</i>	Foresteria		X	Y	McBride et al. (2020)
<i>Geranium carolinianum</i>	Carolina geranium	X			Setzer (2018)
<i>Guaiaacium angustifolium</i>	Texas lignum-vitae	X			McBride et al. (2020)
<i>Gutierrezia microcephala</i>	Threadleaf snakeweed		X		McBride et al. (2020)
<i>Helianthus annuus</i>	Common sunflower	X	X	Y	Foster and Duke (2000)
<i>Heliotropium curassavicum</i>	Salt marsh heliotrope	X	X		McBride et al. (2020)
<i>Heterotheca subaxillaris</i>	Camphorweed	X	X		McBride et al. (2020)
<i>Ibervillea tenella</i>	Basalm gourd	X		Y	McBride et al. (2020)
<i>Ilex vomitoria</i>	Yaupon	X			Foster and Duke (2000)
<i>Jatropha dioica</i>	Leatherstem	X		Y	McBride et al. (2020)
<i>Juniperus ashei</i>	Ashe juniper		X		Moerman (1996)
<i>Juniperus pinchotii</i>	Redberry juniper		X		Setzer (2018)
<i>Karwinskia humboldtiana</i>	Coyotillo	X			McBride et al. (2020)
<i>Larrea tridentata</i>	Creosote bush	X			McBride et al. (2020)
<i>Lepidium latifolium</i>	Broad pepperweed	X	X	Y	Rajeswari (2014)
<i>Lepidium nitidum</i>	Pepperweed		X	Y	McBride et al. (2020)
<i>Lonicera japonica</i>	Japanese honeysuckle		X		Foster and Duke (2000)
<i>Lophophora williamsii</i>	Peyote	X			McBride et al. (2020)
<i>Ludwigia octovalvis</i>	Mexican primrose-willow	X			McBride et al. (2020)
<i>Malva neglecta</i>	Buttonweed		X		Foster and Duke (2000)
<i>Malva parviflora</i>	Little mallow	X			Foster and Duke (2000)
<i>Malvaviscus arboreus</i>	Turkscap	X			McBride et al. (2020)
<i>Matricaria discoidea</i>	Pineappleweed	X	X		Foster and Duke (2000)
<i>Medicago polymorpha</i>	Bur clover	X		Y	Setzer (2018)
<i>Medicago sativa</i>	Alfalfa	X	X		Foster and Duke (2000)
<i>Nicotiana glauca</i>	Tree tobacco	X			McBride et al. (2020)
<i>Oenothera albicaulis</i>	White evening primrose		X		Borchers et al. (2000)
<i>Oenothera rosea</i>	Rose evening primrose	X			Borchers et al. (2000)
<i>Onopordum acanthium</i>	Scotch thistle	X	X		McBride et al. (2020)
<i>Opuntia lindheimeri</i>	Texas pricklypear	X	X	Y	Foster and Duke (2000)
<i>Papaver rhoeas</i>	Common poppy	X			McBride et al. (2020)
<i>Parthenium hysterophorus</i>	Famineweed	X	X		McBride et al. (2020)
<i>Pellaea atropurpurea</i>	Purple cliffbrake		X		McBride et al. (2020)
<i>Plantago rhodosperma</i>	Redseed plantain	X	X	Y	Setzer (2018)
<i>Portulaca oleracea</i>	Purslane	X	X	Y	Foster and Duke (2000)
<i>Prosopis glandulosa</i>	Honey mesquite	X	X	Y	McBride et al. (2020)
<i>Prunus serotina</i>	Wild cherry	X			Setzer (2018)
<i>Pseudognaphalium canescens</i>	Wright's cudweed	X	X		Foster and Duke (2000)
<i>Rhizophora mangle</i>	Red mangrove	X			McBride et al. (2020)
<i>Rhus trilobata</i>	Skunkbush		X	Y	Moerman (1996)
<i>Ricinus communis</i>	Castor bean	X			Foster and Duke (2000)
<i>Rivina humilis</i>	Pigeonberry	X			McBride et al. (2020)
<i>Rumex crispus</i>	Curly dock	X	X		Foster and Duke (2000)
<i>Rumex hymenosepalus</i>	Arizona dock		X		McBride et al. (2020)
<i>Ruta graveolens</i>	Rue	X			McBride et al. (2020)
<i>Salvia texana</i>	Salvia	X		Y	Foster and Duke (2000)

TABLE 1. Continued.

Scientific name	Common name	Rio Grande Plains	Rolling Plains	Bobwhite diet	Source
<i>Senecio flaccidus</i>	Threadleaf groundsel	X			McBride et al. (2020)
<i>Sida abutilifolia</i>	Spreading fanpetals	X		Y	McBride et al. (2020)
<i>Sida rhombifolia</i>	Arrowleaf sida	X			McBride et al. (2020)
<i>Solanum douglasii</i>	Doglas nightshade	X			McBride et al. (2020)
<i>Solanum eleagnifolium</i>	Silverleaf nightshade	X	X		Setzer (2018)
<i>Solanum rostratum</i>	Buffalobur		X	Y	Rajeswari (2014)
<i>Sonchus asper</i>	Spiny sowthistle	X	X		McBride et al. (2020)
<i>Sonchus oleraceus</i>	Sowthistle	X	X		McBride et al. (2020)
<i>Sonchus tenerrimus</i>	Slender sowthistle	X	X		Foster and Duke (2000)
<i>Stellaria media</i>	Chickweed	X			McBride et al. (2020)
<i>Stylosanthes viscosa</i>	Sticky stylo	X			McBride et al. (2020)
<i>Tagetes erecta</i>	Mexican marigold	X	X		McBride et al. (2020)
<i>Taraxacum officinale</i>	Dandelion	X	X		McBride et al. (2020)
<i>Tithonia diversifolia</i>	Mexican sunflower	X	X		McBride et al. (2020)
<i>Toxicodendron radicans</i>	Eastern poison ivy		X		Foster and Duke (2000)
<i>Triticum aestivum</i>	Wheat	X	X	Y	McBride et al. (2020)
<i>Trixis californica</i>	American threefold	X			McBride et al. (2020)
<i>Turnera diffusa</i>	Damiana	X			McBride et al. (2020)
<i>Typha latifolia</i>	Cattail	X	X		Foster and Duke (2000)
<i>Verbascum thapsus</i>	Common mullein	X			Foster and Duke (2000)
<i>Xanthium strumarium</i>	Cocklebur	X	X		Foster and Duke (2000)

up the lacrimal ducts, and into the eye of the bobwhite where they mature into adult eyeworms. Thus, eyeworm larvae, once ingested, are only exposed to plant material found in the bobwhite diet while in the crop. In contrast,

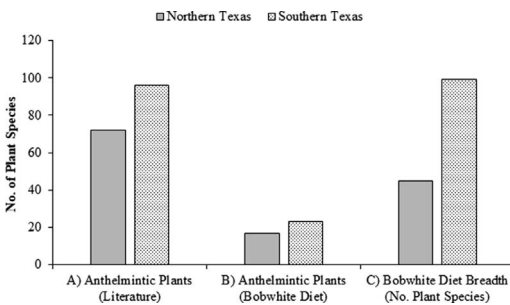


FIGURE 2. Number of plants potentially possessing anthelmintic properties in Texas, USA, found in (A) literature search, and (B) northern bobwhite (*Colinus virginianus*) diet in northern (Rolling Plains and Cross Timbers and Prairies) and southern (Rio Grande Plains) areas of Texas. (C) Diet breadth (number of plants species) of northern bobwhite in northern and southern Texas. Data for the bobwhite diet were obtained from Rollins (1980), Ault (1981), Campbell-Kissock et al. (1985), Wood et al. (1986), and Lehmann and Ward (1941).

cecal worm larvae in intermediate hosts proceed down the digestive tract from crop to gizzard to small intestine and eventually to the ceca, where they live as adults. Cecal worms therefore spend a major portion of their life within the digestive tract of bobwhites where they are exposed to the bobwhite diet. Thus, it is possible that cecal worms might have developed a natural resistance to the potential phytochemicals of anthelmintic plants found in the bobwhite diet. Resistance to phytochemicals by intestinal parasites has been suggested to occur in other species such as the Greater Sagegrouse (*Centrocercus urophasianus*; Fremgen 2015). Fremgen (2015) stated that intestinal parasites in sage-grouse were regularly exposed to plant secondary metabolites from sagebrush and thus may have evolved resistance against such metabolites. If plants with anthelmintic properties occur in the bobwhite diet, then a similar resistance could have developed in bobwhite cecal worms, thereby possibly explaining the lack of a latitudinal gradient in cecal worm prevalence in Texas.

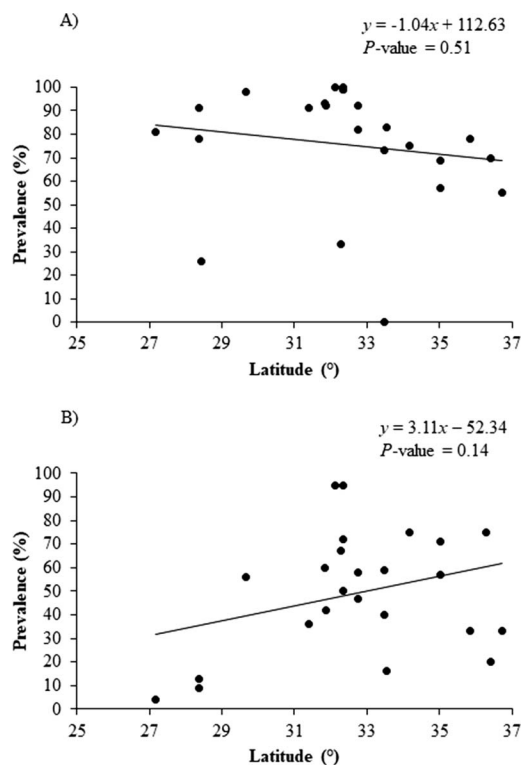


FIGURE 3. Relationship between latitude and prevalence of (A) cecal worm (*Aulonocephalus pennula*) and (B) eyeworm-worm (*Oxyspirura petrowi*) in northern bobwhite (*Colinus virginianus*) in northern (Rolling Plains and Cross Timbers and Prairies) and southern (Rio Grande Plains) Texas, USA, 1980–2020. Data were obtained from nine studies occurring in 24 locations in Texas.

Our study documented circumstantial evidence for the plant-diversity hypothesis as an explanation for the latitudinal gradient in eyeworm prevalence in bobwhites in Texas. The evidence is circumstantial because it is based on correlational evidence and limited data. A comprehensive reference of plants in North America with known anthelmintic properties does not exist, and studies on the bobwhite diet in Texas are few and outdated. Moreover, most studies on eyeworm prevalence in bobwhites have been conducted in localized areas within the Rio Grande Plains or Rolling Plains rather than in a systematic manner across the geographic extent of Texas. Despite these limitations, our evidence suggests that the hypothesis is plausible and warrants experimental testing.

If anthelmintic properties found in diverse plant communities help to combat parasites in northern bobwhite, then the promotion of plant diversity in conservation and management becomes important not only for the provision of habitat for the species but also for directly improving wildlife health.

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SUPPLEMENTARY MATERIAL

Supplementary material for this article is online at <http://dx.doi.org/10.7589/JWD-D-22-00124>.

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