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Helminth parasites of lesser prairie-chicken *Tympanuchus pallidicinctus* in southwestern Kansas: incidence, burdens and effects

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We conducted a 3-year study of helminth parasites to assess their effect on the lesser prairie-chicken *Tympanuchus pallidicinctus*. Helminth parasites were found in most of the examined wild prairie chicken carcasses: 95% had eye worm *Oxyspirura petrowi*, 92% had stomach worm *Tetrameres* sp., and 59% had caecal worm *Subulura* sp. Few parasite burdens or incidences of infection were related to prairie chicken body mass, gender, age or season of collection. Droppings from transmitter-equipped prairie chickens were examined for parasite eggs and the data were used to determine which free-ranging prairie chickens harboured parasites. Telemetry data from 46 heavily parasitized and 52 lightly parasitized or parasite-free prairie chickens indicated no difference between mean daily movements, monthly home ranges, clutch sizes, nest success or survival. No adverse impacts were evident in the lesser prairie-chicken population from the incidences or burdens of the helminth parasites found in our study.

Key words: burdens, effects, helminth parasites, incidence, lesser prairie-chicken, southwestern Kansas, Tympanuchus pallidicinctus

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Incidence and burdens of helminth parasites have been implicated in population declines of grouse, primarily red grouse *Lagopus lagopus scoticus* in Scotland (Hudson 1992). Caecal worm *Trichostrongylus tenuis* burdens have reportedly reduced breeding production (Hudson 1986), increased vulnerability to predators (Hudson, Dobson & Newborn1992a), regulated population cycling (Hudson, Dobson & Newborn 1998) and affected the general behaviour (Fox & Hudson 2001) of red grouse. Parasite burdens may also influence female selection of mates and overall fitness of members of the population (Hillgarth 1990, Robertson & Hillgarth 1994). Few studies in North America have been extensive enough to identify the effects of helminth parasites on critical elements of grouse population dynamics (Peterson 1996). However, recent data suggest that parasite burdens and diseases have the potential to adversely affect small isolated populations of Attwater's *Tympanuchus cupido attwateri* and lesser *T. pallidicinctus* prairie-chickens (Drew, Wigle, Graham, Griffin, Silvy, Fadly

& Witter 1998, Peterson, Purvis, Lichtenfels, Craig, Dronen & Silvy 1998, Hagen, Crupper, Applegate & Robel 2002, Peterson, Ferro, Peterson, Sullivan, Toole & Silvy 2002).

The lesser prairie-chicken is restricted primarily to rangelands dominated by sand sagebrush *Artemisia filifolia*, shinnery oak *Quercus havardii* and bluestem grasses *Andropogon* spp. in eastern New Mexico, southeastern Colorado, western Oklahoma, the Texas panhandle and southwestern Kansas (Giesen 1998). Between 1964 and 1980, lek-count surveys reflected lesser prairie-chicken population declines in southwestern Kansas, primarily because of the conversion of sand sagebrush rangelands into irrigated cropland (Jensen, Robinson & Applegate 2000). Even though the conversion of sandsage habitats into intensive agricultural areas was greatly reduced by the mid 1980s, the indices of lesser prairie-chicken populations continued to decline (Kansas Department of Wildlife and Parks, unpubl. data). The decline of the lesser prairie-chicken reflects that of the nearly extinct Attwater's prairie-chicken, whose population continued to decline in the 1970s after habitat loss, was no longer occurring (Peterson et al. 1998). Kansas Department of Wildlife and Parks personnel (R.D. Applegate, pers. comm.) speculated that helminth parasites might be contributing to the decline of the lesser prairie-chicken populations in Kansas.

Few studies have been conducted on the helminth parasites of lesser prairie-chickens. Braun & Willers (1967) reviewed parasite studies of North American grouse and listed no published reports on helminth parasites in lesser prairie-chickens. Addison & Anderson (1969) found eye worm *Oxyspirura lumsdeni* (now *O. petrowi*) in lesser prairie-chickens from Oklahoma, and Pence & Sell (1979) and Pence, Murphy, Guthery & Doerr (1983) reported eye worm *O. petrowi*, caecal worm *Heterakis isolonchi* and the cestode *Rhabdometra odiosa* in lesser prairie-chickens from Texas. No studies of helminth parasites of lesser prairie-chickens have been conducted in Kansas.

We initiated our study in 1997 to determine the incidence and burdens of helminth parasites in a lesser prairie-chicken population in southwestern Kansas. We also assessed the impacts of helminth parasite burdens on movements, nesting and survival of transmitter-equipped lesser prairie-chickens.

Study area

We conducted the study in southwestern Kansas, primarily in a 7,736-ha fragment of sand sagebrush rangeland in the county of Finney (37° 52' 50" N, 100° 59' 40" W). The soils of the site are sandy of the Tivoli-Dune complex type. The long-term average annual precipitation for the county of Finney was 48 cm with 75% of it occurring during March - August and the mean annual temperature was 12.7°C, ranging from -6.1°C for January to 26.0°C for July.

The rangeland is dominated by sand sagebrush interspersed with grasses such as bluegrama *Bouteloua gracilis*, sand dropseed *Sporobolus cryptandrus*, prairie sandreed *Calamovilfa longifolia*, sand bluestem *Andropogon halii* and little bluestem *Schizachyrium scoparium*. Other plants common on the area include western ragweed *Ambrosia psilostachya*, annual erigonum *Erigonum annum*, plains yucca *Yucca glauca*, prickly pear *Opuntia polyacantha* and Russian thistle *Salsola kali* (Kuchler 1974, Hulett, Tomelleri & Hampton 1988). Over 90% of the sandsage rangeland study site is grazed all year round by cattle. Irrigated cropland surrounding the sandsage rangeland is predominantly devoted to the production of corn *Zea mays*, alfalfa *Medicago sativa* and wheat *Triticum aestivum*.

Ring-necked pheasants *Phasianus colchicus* and northern bobwhites *Colinus virginianus* are other Galliformes commonly found on or adjacent to the sandsage rangeland study area.

Methods

Incidence and burdens of helminth parasites were identified in wild prairie chickens collected in the counties of Finney and Morton during December and January 1997/98 and 1998/99, and in May and October 1998. Birds from the December and January samples were received from hunters whereas those obtained in May and October were birds shot or trapped on leks. Most birds were fully intact when received, i.e. unskinned with head, wings and legs attached. However, some specimens were skinned carcasses without head, wings or legs, and a few consisted of viscera only.

Gender, age and body mass were determined for each intact specimen. Gender and age of specimens were identified by plumage characteristics (Ammann 1944, Copelin 1963) or gonadal examination, when plumage was not present. All specimens were stored frozen until examined for helminth parasites.

Specimens were thawed before being examined visually for helminth parasites using an illuminated stereo binocular microscope. Heads were checked for helminths under eyelids and nictitating membranes and in excised lacrimal ducts. Viscera were removed from the carcasses and extended to separate organ systems. Tracheae were slit longitudinally and examined under magnification for attached helminths. Esophagi and crops were slit longitudinally, rinsed with tap water and examined for attached helminth parasites. The rinsed water was passed through a set of Newark No. 20, 40, and 60 sieves and the residue inspected for helminth parasites. Proventriculi walls were observed carefully for imbedded helminths. Gizzards were cut open and their contents rinsed through sieves to isolate helminth parasites; then their muscular and grinding linings were separated and examined for helminths. The small and large intestines were inspected separately from the caeca; each was flushed and the rinse was passed through sieves and searched for helminths. Intestinal sections and caeca were then slit longitudinally and examined under magnification for attached helminth parasites.

Helminth parasites were cleared with lactophenol and identified following Soulsby (1982) and Ruff (1984). Recovered helminths were preserved in 70% ethanol. Representative specimens of each species of helminth parasite recovered were deposited in the U.S. National Parasite Collection (Beltsville, Maryland, USA) and the Kansas State University Veterinary Parasite Collection (Manhattan, Kansas, USA).

We quantified helminth parasite egg numbers in faecal and caecal droppings to estimate parasite incidence and burdens in the lesser prairie-chicken population. Droppings were collected in May, September and October 1997 and monthly from January 1998 through July 1999, primarily by daytime searches of the sandsage habitat for roosting sites where lesser prairie-chickens commonly defecated, and by flushing transmitter-equipped lesser prairie-chickens at night and collecting droppings at the evacuated flush sites. Occasionally, droppings were collected during spring and fall from sites of lesser prairie-chicken lek activity. Samples were placed in plastic bags and refrigerated until examined for parasite eggs within five days after collection.

Parasite eggs were separated from faecal and/or caecal material by flotation using a modified Wisconsin technique (Foreyt 1990). Parasite eggs collected on cover slips from the surface of sugar solutions in centrifuge tubes were placed on glass slides and examined under a 100x microscope. Eggs were identified following Soulsby (1982) and Ruff (1984) and a comparison was made with eggs from recovered gravid females. Egg counts were converted to eggs-per-gram (EPG) of droppings (Foreyt 1990).

A study of confined lesser prairie-chickens with known burdens of helminth parasites (Walker 2000) determined that parasite eggs in droppings reflected heavy parasite burdens (≥ 4 *Oxyspirura*, 11 *Tetrameres* or 9 *Subulura* worms) whereas droppings without parasite eggs were produced by birds lacking parasites or with light parasite burdens (≤ 5 *Oxyspirura*, 12 *Tetrameres* or 10 *Subulura* worms). We used the presence or absence of parasite eggs in droppings to separate our free-living transmitter-equipped lesser prairie-chickens into two categories: heavily parasitized (termed parasitized hereafter) and parasite-free or lightly parasitized (termed non-parasitized hereafter) birds.

Mean daily movements of transmitter-equipped prairie chickens were estimated by measuring the distance in metres (m) between consecutive daily telemetry locations and calculating a mean of the number of consecutive daily locations (m/day). Daily movements were estimated on a monthly basis only when the number of consecutive daily locations for a bird within a month was ≥ 15. Sizes of monthly home ranges were estimated from telemetry locations using the 95% fixed kernel method (Worton 1989). Monthly home ranges were estimated only for birds for which ≥ 20 locations were available within a given month. We estimated 8-month survival curves (April - November) using the Kaplan-Meier method (Kaplan & Meier 1958) with staggered entry (Pollock, Winterstein, Bunck & Curtis 1989) based on telemetry data from transmitter-equipped birds, and examined the resulting point estimates using log-rank tests (Pollock et al. 1989). Clutch sizes were determined by counting egg shells in completed lesser prairie-chicken nests. Apparent nest success (proportion of nests in which at least one egg successfully hatched) was determined by monitoring activities of nesting transmitter-equipped hens.

We examined the probability of helminth parasite incidence in relation to age and gender of lesser prairie-chickens using 2 x 2 χ^2-contingency tables. We evaluated the relationships between parasite burdens with age and gender using Analysis of Variance (ANOVA). To test for seasonal and sampling (i.e. visceral and dropping samples) differences in helminth species occurrence in lesser prairie-chickens, we used χ^2-contingency tests. One-way ANOVA was used to examine the effects of helminth parasites on body mass and clutch size. We used repeated measures ANOVA to analyze differences in daily movements and monthly home ranges of parasitized and non-parasitized birds. Each bird was considered an experimental unit upon which repeated measures were recorded, and Satterthwaite's approximation was used to estimate the F-test denominator degrees of freedom (Satterthwaite 1946). A 2 x 2 χ^2-contingency test was used to compare the likelihood of nest success of non- and parasitized hens. Because of small sample sizes and

Table 1. Incidence and burdens of helminth parasites recovered from heads and viscera of lesser prairie-chickens collected in southwestern Kansas during 1997-1999. Numbers of paired values in a column sharing the same letter do not differ (P > 0.10).

Specimen category	*Oxyspirura petrowi* Infected N	Infected %	Burden Range	Burden $\bar{x}$	*Tetrameres* sp. Infected N	Infected %	Burden Range	Burden $\bar{x}$	*Subulura* sp. Infected N	Infected %	Burden Range	Burden $\bar{x}$
All birds	56	95	1-81	14	88	92	1-66	21	91	59	1-319	28
Adults	30	100 A	2-32	9 A	43	91 A	1-59	17 A	45	47 A	1-22	18 A
Juveniles	23	91 B	1-81	21 B	33	91 A	3-66	24 B	35	71 B	1-319	30 A
Males	46	93 A	1-81	13 A	62	100 A	1-61	20 A	63	56 A	1-319	26 A
Females	10	100 A	4-51	17 A	23	70 A	3-66	23 A	25	68 A	1-199	34 A

high variances in the data collected, we accepted P = 0.10 as our level of significance, and present actual probability estimates where appropriate.

Results

We collected whole or partial carcasses of 93 lesser prairie-chickens and examined heads and viscera for helminth parasites; and 843 droppings of lesser prairie-chickens were collected and examined for helminth parasite eggs.

Findings of visceral examination

Not all of the lesser prairie-chicken carcasses were whole and intact when collected; four were headless, the caeca of two birds were missing and the viscera of five were too damaged to provide meaningful data. We failed to examine the heads of the first 33 lesser prairie-chickens processed. Therefore, sample sizes for lesser prairie-chicken heads, intestinal tracts and caeca differ.

Eye worm *Oxyspirura petrowi* was found in 53 of 56 lesser prairie-chicken heads examined (Table 1). Burdens of *O. petrowi* in infected birds ranged within 1-81. The incidence of *O. petrowi* infections was greater in adults than in juveniles ($\chi^2 = 2.71$, df = 1, P = 0.100), but the mean burden was greater in juveniles than in adults (F = 7.16, df = 1, 49, P = 0.010). Neither incidences nor burdens of *O. petrowi* differed between male and female lesser prairie-chickens (see Table 1).

Of the 88 lesser prairie-chickens examined, 81 had stomach worm *Tetrameres* sp. Only adult female *Tetrameres* sp. were found, and burdens ranged within 1-66 for infected birds (see Table 1). The incidence of *Tetrameres* sp. infections was identical for adult and juvenile birds, but the mean burden in juveniles (24) was higher than in adults (17; F = 3.51, df = 1, 67, P = 0.065). No gender-related differences were detected in the incidences or burdens of *Tetrameres* sp. in lesser prairie-chickens (see Table 1).

Caecal worm *Subulura* sp. was recovered from caeca of 54 of 91 lesser prairie-chickens examined (see Table 1). Burdens of *Subulura* sp. ranged within 1-319 in infected birds ($\bar{x}$ = 28). There were no differences in incidences or burdens of *Subulura* sp. between adult and juvenile or between male and female lesser prairie-chickens (see Table 1).

The mean body mass (± SE) of 51 whole carcasses of male lesser prairie-chickens was 772 ± 6 g, which was greater (F = 30.92, df = 1, 66, P < 0.001) than the 709 ± 10 g of 17 females. No significant relationships were detected between helminth parasite burden and lesser prairie-chicken biomass. Lesser prairie-chicken with higher numbers of *O. petrowi* had slightly lower body masses, but the relationship between *O. petrowi* burden and body mass was not significant for males or females (Table 2). Males with higher burdens of *Tetrameres* sp. and *Subulura* sp. had slightly lower body masses than males with lower burdens, but the relationship between parasite number and body mass was not significant (see Table 2). Female lesser prairie-chickens with higher burdens of *Tetrameres* sp. and *Subulura* sp. had slightly higher body masses than birds with lower burdens, but the relationship was not significant (see Table 2). When numbers of the three genera of helminth parasites recovered from each bird were combined, the total number of parasitic worms in each bird was not related to body mass of male (N = 51, r = -0.09, P = 0.543) or female (N = 17, r = 0.22, P = 0.406) lesser prairie-chickens.

Viscera of lesser prairie-chicken were collected pri-

Table 2. Correlations between number of helminth parasites recovered during examinations of head and viscera of lesser prairie-chickens and body mass of the birds from southwestern Kansas during 1997-1999.

Parasites	Helminth burden N	Helminth burden Range	Body mass (g) Range	r	P
Oxyspirura petrowi	53	1-81	670 - 880	-0.15	0.306
Males	43	1-81	675 - 880	-0.04	0.821
Females	10	4-51	670 - 755	-0.30	0.404
Tetrameres sp.	63	1-66	670 - 880	0.04	0.744
Males	48	1-61	675 - 880	-0.09	0.524
Females	15	1-66	670 - 755	0.21	0.451
Subulura sp	67	1-319	670 - 880	0.03	0.828
Males	50	1-319	675 - 880	-0.01	0.965
Females	17	1-89	670 - 755	0.21	0.429

Table 3. Seasonal distribution of incidences of helminth parasites recovered from viscera and parasite eggs in faeces of lesser prairie-chickens in southwestern Kansas during 1997-1999. N gives the number of viscera or faecal droppings examined, and % the percentage of viscera or faecal droppings examined that contained helminths or eggs. Numbers in a column sharing the same letter do not differ (P > 0.10). Viscera were not collected during the summer period.

	Oxyspirura petrowi				*Tetrameres* sp.				*Subulura* sp.			
	Viscera		Faeces		Viscera		Faeces		Viscera		Faeces	
Season	N	%	N	%	N	%	N	%	N	%	N	%
Spring	13	92 A	261	6 A	12	100 A	261	41 A	11	18 A	261	<1 A
Summer	-	-	223	1 B	-	-	223	24 B	-	-	223	<1 A
Fall	10	100 A	160	1 B	11	100 A	160	24 B	11	73 B	160	0 A
Winter	32	94 A	199	9 A	61	89 B	199	41 A	65	63 B	199	1 A

marily during four periods: winter 1997/98 (N = 39), spring 1998 (N = 10), fall 1998 (N = 11) and winter 1998/99 (N = 28). The parasite data for the four collection periods were pooled by season for analysis (Table 3). The incidence of *O. petrowi* in lesser prairie-chickens ranged from 92% in spring to 100% in fall, but did not differ by season ($\chi^2 = 1.27$, df = 2, P = 0.529). The incidence of *Tetrameres* sp. infections ranged from 89% in winter to 100% in spring and fall, and differed by season ($\chi^2 = 4.71$, df = 2, P = 0.095). The incidence of *Subulura* sp. was 18% in spring, which was significantly lower than the 73% in fall ($\chi^2 = 6.99$, df = 1, P = 0.008) and the 63% in winter ($\chi^2 = 8.00$, df = 1, P = 0.005).

Findings of faecal/caecal examination

We collected 843 droppings of lesser prairie-chickens from May 1997 through July 1999. The droppings were from 104 transmitter-equipped birds and an unknown number of unmarked birds. We knew the age of the lesser prairie-chickens producing 255 of the droppings and the gender of birds producing 608 droppings. Eggs of *O. petrowi* were found in 34 (4%), *Tetrameres* sp. in 278 (33%) and *Subulura* sp. in 4 (0.5%) of the droppings examined (Table 4).

We recorded oocysts of the protozoan *Eimeria* spp. in three droppings and eggs of the cestode *Choanotaenia infundibulum* in one dropping; however, because these were identified early in our study and were not encountered again, we question the validity of these data. The identifications could have been incorrect or the droppings may have been contaminated before or during processing. We report the data here for the record.

The estimated mean number of helminth eggs-per-gram (EPG) of infected droppings ranged from 16 for *O. petrowi* to 113 for *Subulura* sp. with data from all samples pooled (see Table 4). No differences were detected in the incidences or EPGs of *O. petrowi* eggs recovered from droppings of male or female lesser prairie-chickens. Because no eggs of *O. petrowi* were recovered from droppings of adults, and only two from juveniles, no age-related statistical comparisons were made. The EPGs of *Tetrameres* sp. eggs in droppings did not differ between adult and juvenile or male and female lesser prairie-chickens, and the incidence of *Tetrameres* sp. eggs in droppings of adults and juveniles did not differ. However, the 34% incidence of *Tetrameres* sp. eggs in droppings from males was greater ($\chi^2 = 4.39$, df = 1, P = 0.036) than the 23% incidence for females (see Table 4). Neither the incidences nor EPGs of *Subulura* sp. eggs in droppings of adults and juveniles or males and females differed (see Table 4).

The incidence of *O. petrowi* eggs in droppings differed by season of collection ($\chi^2 = 26.02$, df = 3, P < 0.001), being greater during spring and winter than during summer and fall (see Table 3). The incidence of *Tetrameres* sp. eggs in droppings also reflected differences associated with seasons ($\chi^2 = 28.12$, df = 3, P < 0.001), with droppings collected in spring and winter having the highest incidence and summer and fall droppings the lowest (see Table 3). No differences ($\chi^2 = 2.47$, df = 3,

Table 4. Incidence and numbers of helminth parasite eggs (EPG) counted during flotation examination of lesser prairie-chicken faecal droppings collected from southwestern Kansas during 1997-1999. Numbers of paired values in a column sharing the same letter do not differ (P > 0.10). *O. petrowi* eggs in adults and juveniles were not compared statistically.

		Oxyspirura petrow		*Tetrameres* sp.		*Subulura* sp.	
Source of faeces	N	% with eggs	$\bar{x}$ egg number	% with eggs	$\bar{x}$ egg number	% with eggs	$\bar{x}$ egg number
All samples	843	4	16	33	55	>1	113
Adults	126	0	0	24 A	27 A	2 A	50 A
Juveniles	129	2	625	28 A	49 A	1 A	270 A
Males	513	4 A	17 A	34 A	47 A	>1 A	49 A
Females	95	1 A	10 A	23 B	31 A	1 A	30 A

Table 5. Mean clutch sizes (± SE; as based on the number of completed clutches counted and nests monitored), nest success (based on the % of completed clutches successfully hatching at least one egg), daily movements (expressed as monthly mean (± SE) in m, the number of bird-months where > 15 consecutive daily locations permitted monthly means to be calculated for a bird), home ranges (expressed as monthly mean (± SE) in ha, the number of bird-months where > 20 radio locations permitted calculation of a home range for a bird) and survival of transmitter-equipped parasitized and non-parasitized lesser prairie-chickens in southwestern Kansas during 1997-1999.

	Transmitter-equipped birds				
	N	Parasitized	N	Non-parasitized	P
Mean clutch size (± SE)	26	10.6 ± 0.5	25	9.7 ± 0.7	0.195
Nest success	26	26.9	25	20.0	0.922
Monthly mean daily movement (m)	30	622 ± 33	31	678 ± 38	0.273
Mean monthly home range (ha)	25	241 ± 27	25	218 ± 24	0.531
Survival	46	0.854 ± 0.056	52	0.761 ± 0.060	0.198

P = 0.480) were found in the incidence of *Subulura* sp. eggs recovered from lesser prairie-chicken droppings collected during the various seasons of the year (see Table 3).

Examination of viscera versus droppings

During each season, from which viscera and droppings were available, higher incidences of helminth parasitism were calculated from examinations of viscera than of droppings (see Table 3). We recovered *O. petrowi* from 51 of 53 (96%) viscera examined, whereas eggs of this helminth were found in only 34 of 439 (8%) droppings. *Tetrameres* sp. were recovered from 77 of 84 (92%) viscera examined, whereas eggs of these helminths were found in only 176 of 439 (40%) droppings. We found *Subulura* sp. in 52 of 87 (60%) lesser prairie-chicken viscera examined compared to *Subulura* sp. eggs in only 2 of 439 (< 1%) droppings examined.

Parasite effects on movements and vital rates

We examined droppings from 104 transmitter-equipped lesser prairie-chickens to categorize them as parasitized or non-parasitized. Telemetry data from the birds were used to estimate their daily movements, home ranges, clutch sizes, nest success and survival rates. Data were first analyzed separately by year, but when the annual effects proved non-significant, data from the three years were pooled and analyzed to compare activity and vital rates of parasitized and non-parasitized birds (Table 5).

Clutch sizes of 26 parasitized hens did not differ from those of 25 non-parasitized birds (F = 0.53, df = 1, 49, P = 0.469). The nest success of the 26 parasitized birds was slightly greater than that of the 25 non-parasitized birds, but the difference was not significant ($\chi^2 = 0.019$, df = 1, P = 0.922). The monthly mean movement of parasitized lesser prairie-chickens did not differ from that of non-parasitized birds (F = 1.22, df = 1, 68.7, P = 0.273). No difference was detected between the mean monthly home ranges of parasitized and non-parasitized lesser prairie-chickens (F = 0.40, df = 1, 81.9, P = 0.531). The April - November survival of 46 parasitized lesser prairie-chickens was 0.854, and did not differ from the 0.761 survival of 52 non-parasitized birds ($\chi^2 = 1.653$, 1 = df, P = 0.198; see Table 5).

Discussion

We recovered helminth parasites from all of the whole lesser prairie-chicken carcasses examined. This 100% incidence of infection in Kansas lesser prairie-chickens is consistent with results reported by Pence et al. (1983) for lesser prairie-chickens from Texas.

The incidence (95%) and burdens (1-81) of *O. petrowi* infections were greater in our study than the incidences (57 and 61%, respectively) and burdens (1-9 and 1-19, respectively) of *O. petrowi* reported by Pence & Sell (1979) and Pence et al. (1983), in lesser prairie-chickens from Texas. Addison & Anderson (1969) reported *O. lumsdeni* (now *O. petrowi*) in lesser prairie-chickens from Oklahoma, but incidences and burdens were not quantified. The differences in infection rates of *O. petrowi* in Kansas and Texas lesser prairie-chickens could result from differences in the population densities or food habits of the birds, or differences in the availability of the intermediate hosts of *O. petrowi* in the foraging areas of the birds.

Stomach worms recovered from lesser prairie-chickens in Texas were larval forms of *Physaloptera* sp. (Pence & Sell 1979, Pence et al. 1983), whereas we found adult *Tetrameres* sp. in the lesser prairie-chickens from Kansas. We have no explanation for the differences in the genera of stomach worms found in lesser prairie-chickens from Texas and Kansas. Because insects serve as intermediate hosts of stomach worms (Ruff 1984), it is possible that differences in intermediate host specificity and the ranges of the insects may be responsible for the difference observed. We hesitate to speculate on cause-specific reasons for the differences, because little is known about the life cycles of these parasites in wild lesser prairie-chicken populations. We recovered only female *Tetrameres* from our lesser prairie-chickens. Because species-specific identification of this genus relies heavily on measurements of male structures, we are reluctant to provide a species name. The U.S. National Parasite Laboratory (USDA, Beltsville, Maryland, USA) speculated that the *Tetrameres* sp. we recovered were either *T. pattersoni* or *T. americana* (J.M. Kinsella, pers. comm.).

The incidence and burdens of caecal worms in lesser prairie-chickens from Kansas (59% and 1-319, respectively) were similar to the incidence (60 and 51%, respectively) and burdens (7-267 and 1-271, respectively) of caecal worms reported by Pence & Sell (1979) and Pence et al. (1983), in lesser prairie-chickens from Texas. However, we found *Subulura* sp. in the caecae of our birds, whereas the caecal worms in lesser prairie-chickens from Texas were *Heterakis isoloche*. Hansen & Robel (1972) and Parmalee (1952) found *Subulura brumpti* in northern bobwhites *Colinus virginianus* from Kansas and Texas, respectively. However, the spicule lengths of male *Subulura* specimens that we recovered from lesser prairie-chickens in Kansas were much shorter than *S. brumpti*, and the females were larger than the ranges listed for *S. brumpti*, *S. differens* or *S. strongylina*. Our *Subulura* sp. closely resembled *S. suctoria* of Eurasia (J.M. Kinsella, pers. comm.) and may thus have been that species or a new species.

Pence & Sell (1979) and Pence et al. (1983) found a cestode (*Rhabdometra odiosa*) in 30 and 37%, respectively, of the Texas lesser prairie-chickens they examined. We recovered no cestodes from carcasses of Kansas lesser prairie-chickens. Greater prairie-chickens *Tympanuchus cupido pinnatus* harbour *Raillietina* and *Choanotaenia* in Illinois (Leigh 1940) and Kansas (Harper, Klataske, Robel & Hansen 1967), and *Raillietina* in Wisconsin (Morgan & Hamerstrom 1941). Sharp-tailed grouse *T. phasianellus* harbour *Rhabdometra* and *Choanotaenia* in Wisconsin (Morgan & Hamerstrom 1941) and *Raillietina* and *Rhabdometra* in North Dakota (Aldous 1943). That we failed to recover cestodes from Kansas lesser prairie-chickens is thus surprising.

The presence of *O. petrowi* eggs in droppings was positively correlated ($r = 0.30$) with the number of worms recovered from captive birds, as were the numbers of *Tetrameres* sp. eggs ($r = 0.78$) and *Subulura* sp. eggs ($r = 0.96$), but the correlations were not all significant. However, our categorizations of parasitized and non-parasitized birds were based on examining multiple droppings from the same birds at monthly intervals (66% from ≥ one month). Detection of eggs in droppings of parasitized birds was 68% when a single dropping sample was examined, and ≥ 86% when ≥ two samples were examined. We acknowledge that our use of presence or absence of parasite eggs in droppings to define parasitized and non-parasitized lesser prairie-chickens was not perfect. Eggs were not detected in droppings of birds in which adult helminth parasites were absent, but occasionally birds with low parasite burdens (especially of *Subulura* sp.) produced droppings with no eggs. Even though our categorization of birds as parasitized and non-parasitized was not mutually exclusive, birds characterized as parasitized definitely had parasites whereas those classified as non-parasitized were free of parasites or had low parasite burdens.

Mean clutch size (10.6 eggs) of parasitized lesser prairie-chicken hens did not differ from that of non-parasitized hens (9.7 eggs). Both of the clutch sizes were within the 8-14 egg ($\bar{x} = 10.4$ eggs) range-wide clutch size for lesser prairie-chickens reported by Giesen (1998). The hatching success of the 75 nests monitored in our study area from 1997 to 2000 was 26.7%, and was similar to the nest success of parasitized (26.9%) and non-parasitized (20.0%) hens for the current study, and the 28% range-wide nest success reported by Giesen (1998).

The mean daily movements found in our study were similar to those reported by Taylor & Guthery (1980), but less than those reported by Riley, Davis, Ortiz & Suminski (1994) for lesser prairie-chickens in Oklahoma and New Mexico, respectively. The monthly home ranges of our birds were generally smaller than the home ranges of lesser prairie-chickens in Colorado (Giesen 1998) and Oklahoma (Taylor & Guthery 1980), but larger than the home ranges in New Mexico (Riley et al. 1994). We expected parasitized lesser prairie-chickens to have longer daily movements and larger home ranges than non-parasitized birds if parasite burdens increased their mobility to satisfy higher energy demands. In contrast, movements and home ranges would be shorter and smaller, respectively, if the parasite burdens resulted in morbidity that reduced mobility. No differences were detected in either daily movements or home ranges. Therefore, we doubt that helminth burdens encountered in our study increased the energy demands of lesser prairie-chickens or resulted in reduced mobility as a result of morbidity.

The helminth burdens of our lesser prairie-chickens did not appear to affect their survival. The 8-month survival estimates of 85% and 76% (77% and 64% extrapolated to 12 months) for parasitized and non-parasitized birds, respectively, may have a positive bias because they do not include mortality of birds prior to collection of droppings. Campbell (1972) estimated a 46% annual (12-months) survival for lesser prairie-chickens in New Mexico, and Jamison (2000) estimated a 47-57% annual survival of lesser prairie-chickens at the same location and during the same time period as our study was conducted in Kansas. Even if our two 8-month survival estimates are overestimates, they each contain the same bias and are comparable for the purposes of our study.

The lack of negative effects of helminths on lesser prairie-chickens in our study is in contrast with data from studies of red grouse in the United Kingdom where caecal worms *Trichostongylus tenuis* reportedly reduce survival and fecundity (Hudson 1986, Hudson et al. 1992a, Hudson, Newborn & Dobson 1992b, Hudson et al. 1998, but see Newborn & Foster 2002). Ruff (1984) reported no pathologic effects on grouse of either *Oxyspirura* eye worms or *Tetrameres* stomach worms. The difference between our results for lesser prairie-chickens in Kansas and those for red grouse in the United Kingdom most likely reflects the species of caecal worm involved and the burdens of the worms. The maximum burden of the caecal worm *Subulura* sp. encountered in our study was 319 in a juvenile male; and the mean burden was 28 worms. Red grouse commonly have caecal worm *T. tenuis* burdens of > 5,000 (Hudson 1986, Hudson et al. 1992a). Additionally, the pathologic effects of the two caecal worms differ. No pathologic effects have been reported for *Subulura* spp. (Ruff 1984), whereas the pathologic effects of *T. tenuis* are well documented (Dobson & Hudson 1992, Hudson et al. 1992b). Therefore, the reason why we detected no negative effects of helminths in our lesser prairie-chickens was probably that the birds were infected with low burdens of worms that cause little pathologic damage. More insight into the potential impacts of the helminths recovered from the lesser prairie-chickens in our study could be gained by conducting experimental studies similar to those of Hudson (1986) and Hudson et al. (1992b).

The apparent negligible impacts of helminth infections on lesser prairie-chickens in southwestern Kansas indicate that the recent continued decline of the population probably is due to other exogenous or endogenous factors. Recent research (C.A. Hagen & J.C. Pitman, unpubl. data) suggests that poor nest success and low chick survival are the factors that contribute the most to the mid-1980s to present decline in the population of lesser prairie-chickens in southwestern Kansas.

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