

CANINE HEARTWORMS IN COYOTES IN ILLINOIS

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ABSTRACT: Canine heartworm (*Dirofilaria immitis*) disease affects wild canids and may be a factor impacting the health and population dynamics of coyotes (*Canis latrans*). Coyotes may serve also as a potential reservoir for transmission of these parasites to domestic dogs. We investigated 920 coyotes harvested by hunters and trappers throughout Illinois (USA) from 1995–1997. The objectives of the study were to: 1) survey the regional prevalence and intensity of heartworms in coyotes in Illinois, 2) determine whether heartworm intensity correlates with physical condition, particularly body weight and winter fat levels, and 3) evaluate the relationship between heartworm infections and the reproductive success of females. Prevalence of heartworms statewide was 16.0%. Prevalence was significantly higher in males (17.7%) than in females (14.1%; $P=0.04$) and was higher in the older age-classes ($P<0.0001$). The regional prevalence of heartworms increased from northern to southern Illinois. Intensity ranged from 1 to 111 with a mean of 8.7 (SD=13.2) worms. Intensities did not differ significantly between sexes ($P=0.53$) or among age-classes ($P=0.84$). Most infected coyotes had low intensity infections, 78.2% carried <12 heartworms, 11.6% had 12–24 worms, and 10.2% were infected with >24 worms. Body weights were not correlated with the presence of heartworms, nor were levels of kidney fat and marrow fat. However, reproductive success was lower in infected females. The percent of yearling females that bred was lower among infected females, as was the number of offspring produced by adults ≥ 3.5 yr old. Our study demonstrates that heavy infections adversely affect fur quality and reduce fecundity of some females, but these effects are small and few coyotes (4.1%) had enough worms to trigger them. Coyote populations have increased in Illinois during the past 20 yr, but prevalence and intensity of heartworm disease appears to have changed little in that period. We conclude that heartworm disease is only a minor factor influencing coyote population dynamics in Illinois.

Key words: Canidae, *Canis latrans*, coyote, *Dirofilaria immitis*, dirofilariasis, disease, heartworm.

INTRODUCTION

Canine heartworm (*Dirofilaria immitis*) is one of the most serious parasitic diseases of domestic and wild canids (Custer and Pence, 1981; Grieve et al., 1983). Heartworms can be a source of morbidity and mortality in some coyote populations, and coyotes may serve as an important reservoir for disease transmission to dogs (Gier et al., 1978; Weinman and Garcia, 1980; Pence and Custer, 1981). Although heartworm infection has been documented from several wild canid species in North America, its prevalence and distribution have been most extensively documented in coyotes (Custer and Pence, 1981).

Heartworms are filarial nematodes transmitted to canid hosts by mosquitoes. Adults typically live in the right heart and pulmonary arteries (Pence and Custer, 1981). Pathologic changes created by heartworms are primarily due to physical

obstruction of the heart chambers, valves, and vessels. Eventually, pulmonary endarteritis and obstructive fibrosis will lead to pulmonary hypertension and heart failure. Obstruction of the capillaries by microfilaria also may play a part in the pathogenesis of the disease (Sutton, 1988; Georgi and Georgi, 1990). Coyotes show less severe pathologic effects from heartworms than dogs (Custer and Pence, 1981). Nevertheless, these parasites may have a greater ecologic impact on highly active wild canids than on domestic dogs by reducing cardiopulmonary function, movements, foraging efficiency, reproduction, and survival (Wixsom et al., 1991; Sacks and Blejwas, 2000).

Numerous studies have documented the prevalence of heartworms in local or regional coyote populations, but few have surveyed large samples of coyotes over multiple years. Further, none has ad-

dressed the potential sublethal effects of heartworm infections on the physical condition and reproductive success of coyotes. Consequently, the effects of this parasite on the health and ecology of coyotes are unclear. We initiated this study to better define the effects of heartworm parasitism on the ecology and population dynamics of Illinois' coyotes regionally and statewide. Our objectives were to: 1) survey regional prevalence and intensity of heartworms in coyotes throughout Illinois, 2) determine whether heartworm intensity correlates with physical condition of coyotes, specifically body weight and winter fat levels, and 3) evaluate the relationship between heartworm infections and the reproductive success of female coyotes.

MATERIALS AND METHODS

Information was collected from 920 coyote carcasses collected from fur buyers, hunters, and trappers throughout Illinois during the 1995–96 and 1996–97 hunting and trapping seasons which extended from November through March each year. The date and county of harvest, sex, skinned body weight (kg), and length (cm) were recorded for each animal. Standardized body weight was calculated as skinned weight/body length. Subcutaneous fat was scored as absent, moderate, or abundant on each animal. The quality of fur (based on density and luster) was scored by experienced fur buyers as excellent, good, fair, or poor. Heart, lungs, female reproductive tracts, and lower canine teeth were collected from each coyote. Kidneys, kidney fat, and bone marrow were collected to assess fat reserves.

All four chambers of each heart were inspected for heartworms by gross examination. Heartworms were counted and sexed based on physical characteristics (Soulsby, 1982). Lungs were inspected for parasites by inserting a small tube into the pulmonary artery and flushing with tap water for a minimum of 3 min. During flushing, lungs were massaged to extrude any parasites. After flushing, pulmonary arteries were dissected and inspected for heartworms. Heartworms were preserved in 70% ethyl alcohol with 5% glycerin.

Age of each animal was determined by first radiographing a lower canine tooth. Juveniles were separated from adults based on the width of the pulp cavity (Kuehn and Berg, 1981). Teeth from adults then were sent to Matson Laboratories (Missoula, Montana, USA) for

more precise ageing by counting cementum annuli (Linhart and Knowlton, 1967).

Skinned body weight, standardized weight, kidney fat index, and percent marrow fat were used as indicators of nutritional condition. The kidney fat index was calculated by dividing the weight of perirenal fat by the weight of the kidneys and multiplying this ratio by 100 (Riney, 1955). Percent marrow fat was estimated by extracting marrow from the middle third of the femur, drying the marrow at 60 C to constant weight, and extracting all lipids using ether (Neiland, 1970). Because the organs and tissues used to assess condition were sometimes missing or damaged, complete data sets were available for 637 coyotes.

Reproductive performance of 184 yearling and adult females was estimated by counting placental scars (Harder and Kirkpatrick, 1994). For certain analyses, coyotes were categorized as breeders or non-breeders, where breeders had one or more placental scars and non-breeders were those lacking scars.

Prevalence, mean intensity, and mean abundance of heartworms as defined by Bush et al. (1997) were calculated for both sexes and each age-class of coyotes. These also were calculated separately for coyotes harvested in each of nine regions to assess geographic patterns statewide (Fig. 1). Regions corresponded with the state's major natural divisions defined by unique combinations of climate, topography, and land use (Schwegman, 1973).

Data were analyzed using the SAS statistical package (SAS Inc., 1995). Chi-square tests were used to test for differences in heartworm prevalence between the sexes and among age-classes and regions. Differences in the intensity of infections among age-classes and among regions were tested using one-way analysis of variance (ANOVA). The 2-sample *t*-test was used to compare mean intensities in males and females (Sokal and Rohlf, 1995). We initially divided our sample into infected and uninfected groups to test whether heartworms affect body weight, fat reserves, and fecundity using *t*-tests. Subsequently, we tested whether large numbers of heartworms affected these parameters by subdividing the sample into two groups, those with 0–12 heartworms/coyote and those with ≥ 12 and applying *t*-tests. The latter group comprised only 4.1% of all coyotes. Sample sizes varied among tests because individual organs and tissues could not be used when they were damaged during harvest.

RESULTS

Prevalence and intensity of heartworms

Heartworms were recovered primarily from the right ventricle and pulmonary ar-

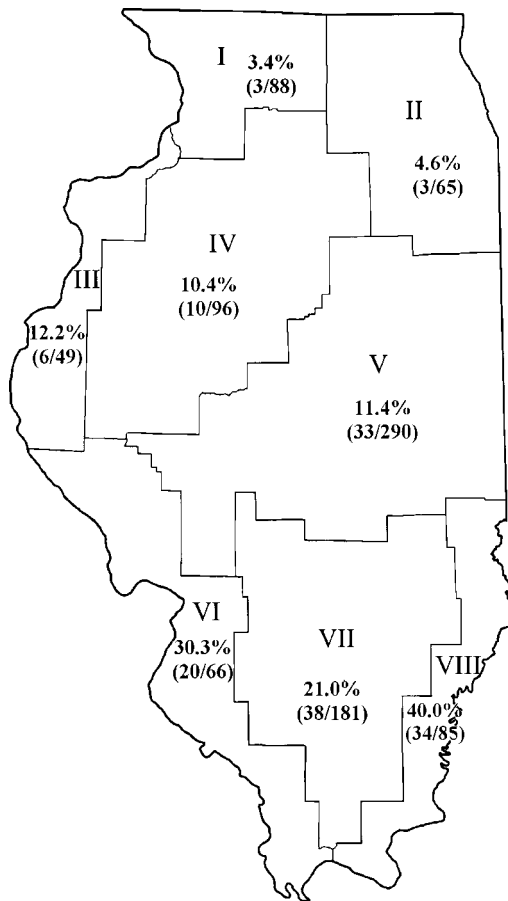


FIGURE 1. Regional prevalence of heartworm in coyotes collected in Illinois, 1995–1997.

tery and to a lesser extent from the right atrium, vena cava, and jugular veins. Statewide, 16.0% of 920 coyotes ranging in age from 0.5 to 13.5 yr were infected with adult heartworms. The prevalence differed significantly among age-classes ($\chi^2=78.6$, $P<0.0001$), increasing with age (Table 1). Prevalence was lowest among juveniles

(8.7%) and highest among adults ≥ 3.5 years old (40.4%). The prevalence of heartworms was significantly higher in males (17.7%) than in females (14.1%) among coyotes of all ages ($\chi^2=4.1$, $P=0.04$).

The prevalence of heartworms differed regionally ($\chi^2=84.2$, $P<0.0001$) ranging from 3.4% in the northwest to 40.0% in the counties bordering the Wabash River in the southeast (Fig. 1). Prevalence was highest in southern Illinois and declined with increasing latitude. The sex-age structure of our sample did not differ among regions ($\chi^2=60.6$, $P=0.12$), therefore regional differences in prevalence were not artifacts of the composition of the samples. The prevalence of heartworms was similar in 1995–96 and 1996–97 and did not differ in any of the nine regions between years ($P=0.12$ –0.82).

The mean abundance of heartworms statewide was 1.5/coyote (SD=6.3). Abundance followed a typical negative binomial distribution (Fig. 2). The number of heartworms in infected coyotes ranged from 1–111 worms with a mean intensity of 8.7 (SD=13.2) worms. The ratio of female to male heartworms was 1.07:1 which did not differ significantly from unity ($P=0.14$). Approximately 81% of infected coyotes contained mature worms of both sexes.

Heartworm intensities did not differ among age-classes ($P=0.84$); juveniles averaged 7.0, yearlings averaged 8.1, and adults averaged 9.4 heartworms/coyote. Across all age-classes, heartworm intensity did not differ between males and females ($t=0.64$; $P=0.53$). Males averaged 9.2 heartworms/infected coyote, whereas fe-

TABLE 1. Age-specific prevalence of heartworms in male and female coyotes harvested statewide in Illinois, 1995–97.

Age (years)	Infected males	Infected females	Total
0.5	21/256 (8.2%)	23/249 (9.2%)	44/505 (8.7%)
1.5	16/86 (18.6%)	12/101 (11.9%)	28/187 (15.0%)
2.5	24/84 (28.6%)	13/50 (26.0%)	37/134 (27.6%)
≥ 3.5	24/54 (44.4%)	14/40 (35.0%)	38/94 (40.4%)
Total	85/480 (17.7%)	62/440 (14.1%)	147/920 (16.0%)

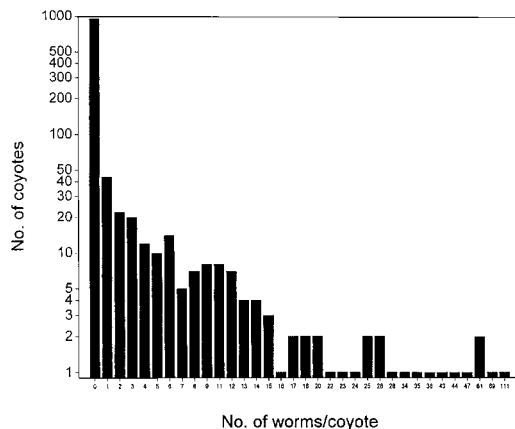


FIGURE 2. Frequency distribution of heartworm abundance in coyotes collected in Illinois, 1995–1997.

males averaged 8.1. Heartworm intensity did not differ among regions ($F=0.24$; $P=0.97$). Most infected coyotes had few worms, 78.2% carried <12 heartworms, 11.6% had 12–24 worms, and 10.2% were infected with >24 worms.

Relationship of heartworm infection and physical condition

The mean skinned body weight of coyotes infected with heartworms did not differ from that of uninfected coyotes in any age class ($P=0.12$ – 0.84), nor was the weight of individuals with high burdens (≥ 12 heartworms) different from those with fewer in any class ($P=0.19$ – 0.79) (Table 2). Similarly, standardized body

weights did not differ between infected and uninfected individuals ($t=-1.41$; $P=0.16$) or between coyotes with high burdens and those with fewer worms ($t=-0.27$; $P=0.79$).

Fur quality differed significantly between infected and uninfected coyotes ($\chi^2=9.97$, $P<0.04$). Fifty-seven percent of uninfected coyotes had coats rated as excellent or good; whereas only 40.0% of infected individuals had fur of this quality. Neither kidney fat index ($F=-0.75$; $P=0.46$) nor percent marrow fat ($F=0.08$; $P=0.77$) differed between infected and uninfected coyotes (Table 2). Coyotes with high heartworm burdens were found to have KFI values similar to those with fewer worms and similar levels of marrow fat (Table 2).

Relationship of heartworm infection and female reproduction

The mean number of placental scars differed among females in the three age-classes ($F=45.9$; $P<0.001$; Table 3). Infected females tended to have fewer scars in all age-classes (Table 3), but this difference was significant only in females ≥ 3.5 -yr old. Only 33.3% of infected yearling females had placental scars, whereas 44.8% of uninfected yearlings had scars ($\chi^2=12.2$; $P=0.02$). Differences in the percentage of females breeding were not found in older classes. We had too few females with

TABLE 2. Comparisons of condition indices for heartworm-infected versus uninfected coyotes and for coyotes with <12 heartworms versus those with ≥ 12 heartworms (Illinois, USA). Sample sizes are shown in parentheses.

Subsample		Skinned body weight (kg)	Standardized body weight ^a	KFI ^b	Percent marrow fat
Uninfected coyotes (<i>n</i> = 517)	<i>x</i>	22.6	0.46	51	87.7
	SD	4.9	0.09	24	10.3
Infected (<i>n</i> = 120)	<i>x</i>	23.7	0.48	49	87.1
	SD	4.8	0.10	25	9.4
<12 worms/coyote (<i>n</i> = 612)	<i>x</i>	22.8	0.47	51	87.2
	SD	4.9	0.10	24	10.4
≥ 12 worms/coyote (<i>n</i> = 25)	<i>x</i>	22.7	0.47	50	87.5
	SD	4.6	0.08	29	4.3

^a Standardized body weight = skinned weight (kg)/body length (cm).

^b Kidney fat index = (weight of kidney fat/weight of kidneys) $\times 100$.

TABLE 3. Comparisons of the mean number of placental scars per breeding female in heartworm-infected versus uninfected female coyotes by age-class in Illinois, USA.

Age-class (years)	<i>n</i>	<i>X</i>	<i>SD</i>	<i>t</i> -value	<i>P</i>
Yearling					
Uninfected coyotes	87	1.9	2.4	1.00	0.34
Infected	9	1.1	2.1		
2 yr old					
Uninfected coyotes	35	3.0	2.8	0.47	0.65
Infected	13	2.5	3.4		
≥ 3 yr old					
Uninfected coyotes	24	6.0	2.4	2.26	0.03
Infected	16	3.8	3.3		

heavy heartworm burdens in each age-class to conduct valid comparisons of fetal rates between females with heavy versus light burdens.

DISCUSSION

Prevalence of heartworm in Illinois' coyotes is relatively high, but it appears to have changed little in the past 20 yr. Kick et al. (1984) surveyed over 400 coyotes collected from 1977 to 1980 and reported that 9.4% of the animals from northern Illinois and 21.8% from southern Illinois were infected with heartworms. They reported a mean intensity of 9.6 heartworms/coyote, similar to the 8.8 that we found. At the time of their study, the enzootic zones for heartworm were expanding north and westward from the gulf coast and the prevalence of the disease in mid-western coyotes had increased greatly during the previous 5–8 yr (Otto, 1975; Kick et al., 1984). Canine heartworm is currently endemic in Illinois in dogs and coyotes, but its prevalence appears to have stabilized at 5–12% in northern and central Illinois and 20–40% in southern Illinois (Kick et al., 1984; Gregory, 1998).

Prior to the 1980s, coyotes were not considered to be a natural host or important reservoir for heartworms; however more recent studies suggest that prevalence may be similar in sympatric coyote and dog populations (Custer and Pence,

1981; Sacks and Blejwas, 2000). This is true in Illinois. A statewide survey conducted concurrently with this study found that 13% of dogs not on preventative medication tested positive for heartworms, similar to the 16.0% that we found in coyotes (Gregory, 1998). Coyotes appear to be an important host for heartworms particularly in southern Illinois and may serve as a reservoir for the transmission of heartworm to domestic dogs.

The geographic pattern we observed, with prevalence increasing from north to south, may result from the longer period of exposure to mosquitoes in the south. A similar pattern has been reported for dogs in Illinois (Marquardt and Fabian, 1966; Gregory, 1998). However, the availability of breeding habitats favored by mosquito vectors also may influence this pattern. Southern Illinois has proportionately more bottomland forests, swamps, and forested wetlands than other regions of the state (Suloway and Hubbell, 1994). These habitats are preferred by three mosquitoes, *Aedes canadensis*, *A. trivittatus*, and *A. vexans*, that have been implicated as vectors for canine heartworm in the midwest (Pappas and Lunzman, 1985; Illinois Department of Public Health, 1995).

Most studies have reported higher prevalence of heartworms in older coyotes and this is usually attributed to increased exposure to infected mosquitoes over the course of their lifetime (Weinmann and Garcia, 1980; Custer and Pence, 1981; Kick et al., 1984). There is no evidence that protective immunity to heartworms develops in coyotes or other canids. Unlike several previous studies (Custer and Pence, 1981; Kick et al., 1984; Pappas and Lunzman, 1985), we did find significant differences in prevalence between males and females. This difference may have been detectable because of our large sample size, which was approximately double that of the previous studies. Male coyotes may be more vulnerable to infection because their movements increase their exposure to mosquito vectors. Adult females

generally restrict their movements during summer when tending pups at the den site; whereas breeding males extend their daily movements at this time (Parker and Maxwell, 1989; Patterson et al., 1999).

We found no relationship between abundance of heartworms and weight of coyotes or winter fat reserves. Attwell (1988) reported infected dogs typically do not lose weight, although it seems reasonable to assume that impacts on highly active predators such as coyotes might be more severe. Sacks and Blejwas (2000) reported body weights at death were lower for a group of heavily infected coyotes and marrow fat was negatively correlated with heartworm burden. Their affected group averaged 34 worms apiece, whereas unaffected individuals averaged four. They speculated that heartworms reduced stamina and foraging efficiency, leading to nutritional stress. We found no evidence of this. However, if heavily infected coyotes reduce their movements, they may be under-represented in harvested samples.

Heartworms might be expected to reduce the reproductive efficiency of coyotes by limiting foraging efficiency, increasing metabolism, or suppressing appetite (Sacks and Blejwas, 2000). Whatever the mechanism, we found that infected females produced fewer fetuses, as indicated by fewer placental scars. Significant relationships between heartworm infections and reproduction were found in yearlings, who comprise a large portion of the population but typically have low natality rates, and adults ≥ 3.5 yr old, who have high natality rates but comprise a small portion of the population. Heartworm infections may reduce the probability of yearlings breeding and the number of fetuses produced by breeding adults.

The negative relationship between heartworm intensity and fur quality suggests a mechanism for parasite-mediated sexual selection in coyotes. Hamilton and Zuk (1982) hypothesized that animals select mates for their genetic resistance to parasites and they do this by scrutinizing phe-

notypic traits that are reliable indicators of health, such as the luster of feathers or fur (Moller et al., 1999). Although we are not aware of any direct relationship between coat quality and breeding status in coyotes, it seems reasonable to speculate that individuals with poor coats may be at a disadvantage during competition for mates.

Heartworm is a chronic debilitating disease that can impact the physiologic condition, reproductive performance, and survival of coyotes. Our study suggests that heavy infections may adversely affect fur quality and reduce fecundity of some females. However, these effects were relatively small and few coyotes (4.1%) carried burdens high enough to trigger them. Therefore, we conclude that heartworm disease is only a minor factor influencing coyote population dynamics in Illinois. Coyote populations have increased in the state over the past 20 yr, but prevalence and intensity of the disease appear to have changed little in that period. Nevertheless, coyotes could be an important potential reservoir for transmission of the disease to dogs, particularly in southern Illinois, and this role should be recognized in developing heartworm control programs.

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LITERATURE CITED

- ATTWELL, R. B. 1988. Clinical signs and diagnosis of canine dirofilariasis. *In* *Dirofilariasis*, P. F. L. Borham and R. B. Attwell (eds.). CRC Press, Boca Raton, Florida, pp. 191–203.
- BUSH, A. O., K. D. LAFFERTY, J. M. LOTZ, AND A. W. SHOSTAK. 1997. Parasitology meets ecology on its own terms: Margolis et al. revisited. *Journal of Parasitology* 83: 575–583.
- CUSTER, J. W., AND D. B. PENCE. 1981. *Dirofilariasis* in wild canids from the Gulf Coastal prairies of

- Texas and Louisiana, U.S.A. *Veterinary Parasitology* 8: 71–82.
- GEORGI, J. R., AND M. E. GEORGI. 1990. *Parasitology for veterinarians*, 5th Edition, W. B. Saunders Co., Philadelphia, Pennsylvania, 412 pp.
- GIER, H. T., S. M. KRUCKENBERG, AND R. J. MARLER. 1978. Parasites and diseases of coyotes. In *Coyotes: Biology, behavior and management*, M. Bekoff (ed.). Academic Press, Inc. New York, New York, pp. 37–71.
- GREGORY, D. G. 1998. Heartworm and lungworms in Illinois' canids. M.S. Thesis, Eastern Illinois University, Charleston, 47 pp.
- GRIEVE, R. B., J. B. LOK, AND L. T. GLICKMAN. 1983. Epidemiology of canine heartworm infection. *Epidemiological Review* 5: 220–246.
- HAMILTON, W. D., AND M. ZUK. 1982. Heritable true fitness and bright birds: A role of parasites? *Science* 218: 384–387.
- HARDER, J. D., AND R. L. KIRKPATRICK. 1994. Physiological methods in wildlife research. In *Research and management techniques for wildlife and habitats*, 5th Edition, T. A. Bookhout (ed.). The Wildlife Society, Bethesda, Maryland, pp. 275–308.
- ILLINOIS DEPARTMENT OF PUBLIC HEALTH. 1995. Mosquitoes in Illinois: Recommendations for prevention and control. Illinois Department of Public Health, Springfield, 28 pp.
- KICK, T. J., G. F. HUBERT, JR., AND R. D. ANDREWS. 1984. Heartworms (*Dirofilaria immitis*) in coyotes (*Canis latrans*) in Illinois. *Transactions of the Illinois State Academy of Sciences* 77: 127–134.
- KUEHN, D. W., AND W. E. BERG. 1981. Use of radiographs to identify age-classes of fisher. *Journal of Wildlife Management* 45: 1009–1010.
- LINHART, S. B., AND F. F. KNOWLTON. 1967. Determining age of coyotes by tooth cementum layers. *Journal of Wildlife Management* 31: 362–365.
- MARQUARDT, W. C., AND W. E. FABIAN. 1966. The distribution of filarids in Illinois' dogs. *Journal of Parasitology* 52: 318–322.
- MOLLER, A. P., P. CHRISTE, AND E. LUX. 1999. Parasitism, host immune function, and sexual selection. *The Quarterly Review of Biology* 74: 3–20.
- NEILAND, K. A. 1970. Weight of dried marrow as indicator of fat in caribou femurs. *Journal of Wildlife Management* 34: 904–907.
- OTTO, G. F. 1975. Changing geographic distribution of heartworm in the United States. In *Proceedings of the heartworm symposium—1974*, H. C. Morgan (ed.). VM Publishing, Inc., Bonner Springs, Kansas, pp. 1–2.
- PAPPAS, L. G., AND A. T. LUNZMAN. 1985. Canine heartworm in the domesticated and wild canids of southeastern Nebraska. *Journal of Parasitology* 71: 828–830.
- PARKER, G. R., AND J. W. MAXWELL. 1989. Seasonal movements and winter ecology of the coyote, *Canis latrans*, in northern New Brunswick. *Canadian Field-Naturalist* 103: 1–11.
- PATTERSON, B. R., S. BONDRUP-NIELSEN, AND F. MESSIER. 1999. Activity patterns and daily movements of the eastern coyote, *Canis latrans*, in Nova Scotia. *Canadian Field-Naturalist* 113: 251–257.
- PENCE, D. B., AND J. W. CUSTER. 1981. Host-parasite relationships in the wild Canidae of North America. II. Pathobiology of infectious diseases in the genus *Canis*. In *Proceedings of the Worldwide Furbearer Conference*, J. A. Chapman and D. Pursley (eds.). Worldwide Furbearer Conference, Frostburg, Maryland, pp. 760–845.
- RINEY, T. 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. *New Zealand Journal of Science and Technology* 36: 428–463.
- SACKS, B. N., AND K. M. BLEJWAS. 2000. Effects of canine heartworm (*Dirofilaria immitis*) on body condition and activity of free-ranging coyotes (*Canis latrans*). *Canadian Journal of Zoology* 78: 1042–1051.
- SAS INCORPORATED. 1995. SAS 6.12. SAS Institute Incorporated, Cary, North Carolina, 373 pp.
- SCHWEGMAN, J. E. 1973. Comprehensive plan for the Illinois Nature Preserve System. Part 2: The natural divisions of Illinois. Illinois Nature Preserve Commission, Rockford, Illinois, 30 pp.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry: The principles and practice of statistics in biological research*, 3rd Edition. W. H. Freeman and Company, San Francisco, California, 887 pp.
- SOULSBY, E. J. L. 1982. *Helminths, arthropods and protozoa of domesticated animals*, 7th Edition, Lea & Febiger, Philadelphia, Pennsylvania, 809 pp.
- SULOWAY, L., AND M. HUBBELL. 1994. Wetland resources of Illinois: An analysis and atlas. Illinois Natural History Survey Special Publication 15, Champaign, Illinois, 88 pp.
- SUTTON, R. H. 1988. Pathology and pathogenesis of dirofilariasis. In *Dirofilariasis*, P. F. L. Boreham and R. B. Attwell (eds.). CRC Press, Boca Raton, Florida, pp. 99–132.
- WALTERS, L. L., AND M. M. J. LAVOPIERRE. 1984. Landscape epidemiology of mosquito-borne canine heartworm (*Dirofilaria immitis*) in northern California USA. I. Community-based surveys of domestic dogs in three landscapes. *Journal of Medical Entomology* 21: 1–16.
- WEINMAN, C. J., AND R. GARCIA. 1980. Coyotes and canine heartworm in California. *Journal of Wildlife Diseases* 16: 217–221.
- WIXSOM, M. J., S. P. GREEN, R. M. CORWIN, AND E. K. FRITZELL. 1991. *Dirofilaria immitis* in coyotes and foxes in Missouri. *Journal of Wildlife Diseases* 27: 166–169.

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