

THE STRUCTURE AND SEASONALITY OF *BAYLISASCARIS PROCYONIS* POPULATIONS IN RACCOONS (*PROCYON LOTOR*)

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ABSTRACT: *Baylisascaris procyonis*, the raccoon (*Procyon lotor*) ascarid, is a common roundworm parasite of raccoons that is also a well-recognized zoonotic pathogen, and a cause for conservation concern. The transmission dynamics of *B. procyonis* differ with host population attributes, season, and landscape. We examined how the parasite's population attributes change with season, parasite population structure, and host demographics. We examined 1,050 raccoon gastrointestinal tracts collected from 1996 to 2012. Of the 1,050 raccoons necropsied, 382 (36%) were infected with at least one *B. procyonis* (\bar{x} =15.8 [95% confidence interval=13.39–18.26]; median=7; range 1–199 worms/host), and populations were overdispersed. There was a seasonal change in prevalence with a peak in October/November. Worm burdens decreased approximately 28% per month from January to June and increased approximately 31% per month from June to December. The sex structure of *B. procyonis* populations was female-biased (56% female). Host demographics did not impact parasite population attributes. This study provides evidence that *B. procyonis* populations exhibit a yearly cycle of loss and recruitment that may impact the transmission dynamics of the parasite.

Key words: *Baylisascaris procyonis*, nematode, population, prevalence, seasonality.

INTRODUCTION

Baylisascaris procyonis, the common ascarid or roundworm of raccoons (*Procyon lotor*), is the most common cause of clinical larva migrans, affecting >130 species of vertebrates (Page 2013). This parasite also is zoonotic and has resulted in over 30 severe or fatal cases of larva migrans over the past 35 yr (Kazacos 2001; Gavin et al. 2005; K.R.K. unpubl. data). Due to the severity of larva migrans, much of the research on *B. procyonis* has focused on determining risk of transmission to children (Sorvillo et al. 2002; Roussere et al. 2003; Page et al. 2009a) or animals of conservation concern (LoGiudice 2003; Page et al. 2012; Smyser et al. 2012). The transmission dynamics fluctuate with host population attributes (Page et al. 2009b), season (Page et al. 2005), and landscape features (Page et al. 2009b, Kresta et al. 2010); however, it is not understood how these fluctuations relate to changes in parasite population size and structure. Understanding the population dy-

namics of *B. procyonis* would allow a more refined understanding of its transmission.

Raccoons are the definitive host of *B. procyonis*. Raccoons become infected when they ingest third-stage larvae that are in the tissues of small vertebrate paratenic hosts, including mice and squirrels (D. Bowman pers. comm.; Kazacos 2001; Smyser et al. 2015a). Juvenile raccoons can additionally become infected when they ingest larvated eggs from latrines or their mother's fur (Kazacos 2001). Because of the multiple modes of infection, prevalence of infection is highest among juvenile raccoons (up to 90%) and young raccoons are considered an important mode of recruitment of the parasite into raccoon populations (Kazacos 2001).

Prevalence of *B. procyonis* infection varies with season (Page et al. 2005) and Kazacos (2001) suggests that the parasite population undergoes a yearly cycle in temperate regions. Studies showing increased prevalence in the fall (Schultz 1962; Smith et al. 1985; Kidder et al. 1989; Page et al. 2005) support the idea of

decreased worm burdens related to a self-cure of raccoons during winter, followed by recruitment and reinfection, especially in young raccoons, in late spring and summer (Kazacos 2001).

Our objective was to examine parasite population attributes across raccoon hosts from raccoons collected opportunistically in the Midwest, US. Specifically, we address the seasonality of infection and shifts in age structure of worm populations as a function of host demographics.

MATERIALS AND METHODS

To describe the population structure of *B. procyonis*, we obtained 1,050 gastrointestinal tracts from road-killed or nuisance-removed raccoons collected over 16 yr (1996–2012) in Illinois, Indiana, Kansas, Michigan, Minnesota, Missouri, and Wisconsin. For each raccoon, we recorded the date and location of collection, sex, and age class, with individuals considered juveniles if they were younger than 1.5 yr. Age was estimated using tooth emergence or wear (Grau et al. 1970). Gastrointestinal tracts were stored at -20 C until necropsy. The intestines were opened longitudinally and the lumen, ingesta, and mucus were examined for parasites. For every host, all *B. procyonis* individuals were counted and measured, and sex was determined to describe the age and sex structure of each population of worms. To assign an age to worms, we used data from a separate set of 55 female worms collected previously (K.R.K. unpubl. data). These worms were used to determine the average length of female worms that had eggs present in their vagina. Eggs were not found in the vagina of worms ≤ 6.3 cm; therefore, worms were considered juvenile if ≤ 6.3 cm.

Yearly trends were not considered in our analysis because the opportunistic sampling strategy did not yield enough data points in multiple years. A plot of prevalence by month suggested a potential cubic trend. This was investigated using beta regression where prevalence was regressed on month, month², and month³. Beta regression assumes a beta distribution for the response (in this case prevalence). Beta distributions can take on a variety of shapes, so they are more flexible in modeling proportion data and do not have the symmetry assumption necessary for ordinary regression. In this implementation of beta regression, two generalized linear models were fit using maximum likelihood with a Newton-Raphson/Fisher scoring algorithm. These two functions

model the mean of the beta distribution with a logit link and the precision of the beta distribution with an identity link. We defined seasons prior to looking at the data. Based on previous knowledge that prevalence of *B. procyonis* infection increases in fall and decreases in summer (Kazacos 2001; Page et al. 2005), we determined that seasons for our analysis would be spring/summer (March–August) and autumn/winter (September–February). Seasonal differences in prevalence due to host sex and age were investigated using *t*-tests. First, the data were split by season. For each season, prevalence was computed for each age group, and a *t*-test was used to test differences in mean prevalence by host age. A similar analysis was performed for host sex.

Potential seasonal components to burden characteristics were analyzed by regressing burden on month using segmented negative binomial regression, as there was graphic evidence of a decreasing trend in burden for the first half of the year and an increasing trend in the second half. In this implementation of segmented regression, a breakpoint was estimated and two negative binomial regression lines were fit on either side of the breakpoint. Negative binomial regression was used as opposed to Poisson or standard linear regression because of concerns of overdispersion of burden counts (Anderson and May 1978). The sample standard deviation of burden counts is approximately three times that of the sample mean. Subsequently host age and sex were added to the original negative binomial regressions to test the significance of these covariates.

For the 1,050 raccoons examined, the average worm length and the percentage of female worms were regressed on month, host sex, and host age using ordinary multiple regression. A drop in average worm length from October to January was investigated via a *t*-test. Additionally, negative binomial regression was used to investigate the relationship of burden to the distribution of female worms in the population. Potential crowding of worms (associated with overdispersion) was investigated by regressing the natural log of burden on the natural log of average worm length. The log transformations were used to better meet the assumption of linearity in ordinary least squares regression.

RESULTS

Of the 1,050 raccoons necropsied, 382 (36%) were infected with at least one *B. procyonis* ($\bar{x}=15.8$; 95% confidence interval [CI]=13.39–18.26; median=7; range 1–199 worms/host; Table 1). The parasites were overdispersed, with only 7% of the infected

TABLE 1. Average parasite burden (among infected animals) and worm lengths (cm) for raccoon roundworms (*Baylisascaris procyonis*) as measured during necropsy of infected raccoon (*Procyon lotor*) hosts in the central USA from samples obtained 1996–2012. Data are presented by host age and sex.

Host characteristic	n	Mean worm burden ±SD	Mean worm length ±SD (cm)
Adult	152	10.46 ± 14.20	9.62 ± 3.83
Juvenile	113	11.90 ± 12.21	8.06 ± 3.27
Female	75	24.39 ± 38.21	8.20 ± 3.09
Male	91	18.44 ± 21.97	8.84 ± 3.85

raccoons having more than 50 worms. A cubic trend in prevalence was detected via beta regression (pseudo- $r^2=0.581$), with prevalence decreasing from approximately October to May and increasing in the summer/early fall months (Fig. 1 and Table 2). There was no evidence of a difference in prevalence due to host age or sex, for either season ($P>0.1$).

Populations of *B. procyonis* ranged from 1 to 199 individuals, and individual worms had an average length of 8.22 cm (95% CI=8.08–8.37). Population size exhibits seasonality with strong evidence for a negative trend from January through June ($P<0.001$; Table 3) and a positive trend from June to December ($P<0.001$; Table 3). On average, raccoons lost approximately 16 worms from January to June, and gained approximately 28 worms from June to December (Fig. 2).

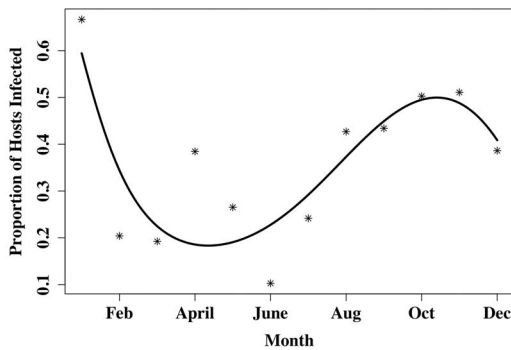


FIGURE 1. Prevalence of *Baylisascaris procyonis* by month in the central USA (1996–2012), with overlaid cubic regression model fit ($n=12$) of the seasonal trend. Prevalence tends to decrease in winter.

TABLE 2. Results of a cubic beta regression of prevalence on month (1996–2012) demonstrate a seasonal trend with a significant cubic component. Prevalence of *Baylisascaris procyonis* tends to decrease in the winter in the central USA.

	Dependent variable: regression coefficient ±SE
Month	-1.827 ± 0.455*
Month ²	0.298 ± 0.079*
Month ³	-0.013 ± 0.004*
Constant	1.925 ± 0.686*
Pseudo- r^2	0.581

* $P<0.01$.

The average length (associated with age) of individuals in *B. procyonis* populations increased 0.27 cm/mo until October ($P=0.001$), and then decreased on average 3.32 cm between October and January (95% CI=1.86–4.79; Fig. 3 and Table 4). There is no evidence that worm length differs as a function of host sex ($P=0.15$) and only weak evidence that it is related to host age ($P=0.07$).

Populations of *B. procyonis* were, on average, 56% female, a difference that was statistically significant ($t=3.69$, $df=292$, $P=0.0001$), and there were no differences in this ratio as a function of host age or sex, or of season ($P>0.17$; linear regression). However, there was evidence that as the percentage of adult female worms in a population increased, there was a reduction in the predicted burden size ($P<0.001$; Table 5). There was no evidence of a crowding effect ($P=0.36$).

TABLE 3. Coefficients from the negative binomial regression for seasonal trend in worm (*Baylisascaris procyonis*) burden in the central USA; burden of hosts (*Procyon lotor*) regressed on months 1–6 and 6–12 (data collected 1996–2012).

	Dependent variable ±SE	
	Burden months 1–6	Burden months 6–12
Month	-0.337 ± 0.076*	-0.318 ± 0.043*
Constant	3.297 ± 0.304*	-0.324 ± 0.422*
Observations	94	299

* $P<0.01$.

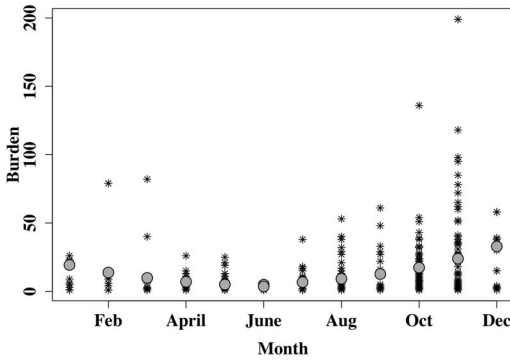


FIGURE 2. Population burden of *Baylisascaris procyonis* by month in the central USA (1996–2012), in number of worms; infected hosts (*Procyon lotor*) only ($n=382$). Asterisks represent individual host burden, and grey circles are the estimated means obtained via the beta regression fit.

DISCUSSION

Seasonal differences in prevalence of *B. procyonis* have been reported (Smith et al. 1985; Kidder et al. 1989; Page et al. 2005; Jardine et al. 2014) and decreases in the winter have been attributed to the loss of worms due to cold stress (LoGiudice 1995; Kazacos 2001). However, the connection between decreased prevalence and declining worm population size has not been reported until now. By looking at numerous worm populations across years, we were able to document a decline in worm population size that coincides with lower prevalence and

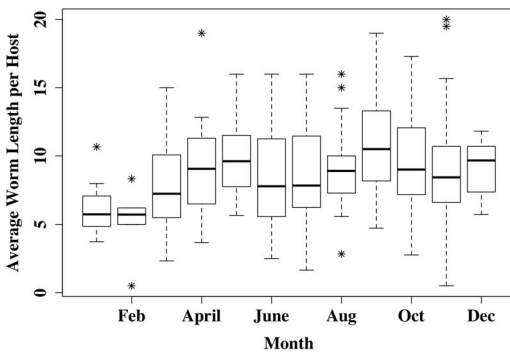


FIGURE 3. Boxplots summarize the average worm (*Baylisascaris procyonis*) lengths (cm) per host (*Procyon lotor*) by month in the central USA (1996–2012). Asterisks represent potential outliers ($n=284$).

TABLE 4. Coefficients from the linear regression for seasonal trend in worm (*Baylisascaris procyonis*) lengths in the central USA; average worm length (cm) regressed on month (January–October only) (data collected 1996–2012).

	Dependent variable: average length \pm SE (cm)
Month	0.271 \pm 0.084*
Constant	7.093 \pm 0.661*
Observations	228
r^2	0.044
Residual SE	3.490 (df=226)
F statistic	10.484 \pm 1; 226*

* $P < 0.01$.

demonstrates that loss of worms continues through June. After June, recruitment of worms results in increasing worm populations from July through December, coinciding with increasing prevalence of infection in hosts. The observed seasonal patterns in worm burden and prevalence may be explained by seasonal changes in latrine use or seasonal shifts in food habits.

Raccoon latrines play an important role in transmission of *B. procyonis* (Page et al. 1999). Transmission occurs when visiting paratenic hosts or juvenile raccoons come into contact with accumulations of fecal material at latrines, which are foci for infective *B. procyonis* eggs (Page et al. 1998). Multiple raccoons may visit a single latrine, and one raccoon may visit up to six latrines in 2 wk (Hirsch et al. 2014); therefore, any seasonal changes in latrine use by raccoons could influence the seasonal dynamics of worm

TABLE 5. Coefficients from the negative binomial regression; host (*Procyon lotor*) burden regressed on percentage of adult female worms (*Baylisascaris procyonis*). Data collected 1996–2012 in the central USA.

	Dependent variable: burden \pm SE
% Female worms	-1.081 \pm 0.204*
Constant	3.483 \pm 0.160*
Observations	264

* $P < 0.01$.

populations. For example, increasing worm population sizes coincides with weaning of young raccoons and increased exploratory behavior (Gehrt 2003). After weaning, young raccoons increase their visitations to latrines and, consequently, increase their exposure to *B. procyonis*. Increased exploratory activity of young raccoons coincides with natural increases of fecal material at latrines as feces accumulations increase at latrines in the fall and decrease through winter and into early spring (L.K.P. pers. obs.)

Seasonal shifts in food preference among raccoon populations could also explain the seasonal patterns observed among *B. procyonis* populations. Investigators have reported raccoons in the Midwest consuming vertebrate prey during spring and early summer, and then shifting nearly exclusively to plants during summer and fall (Stuewer 1943; Greenwood 1981). Adult reinfections may initiate with the shift to vertebrate prey, with the worm population growing as the physical condition of the host improves during summer, and additional infections occurring through communal use of latrines (either directly at the latrines or by occasional consumption of infected intermediate hosts located near latrines) (Kazacos 2001). Most of the raccoons in this study were from the Chicago area, and depend on anthropogenic food sources, including refuse (Gehrt 2004; Prange et al. 2004; Bozek et al. 2007). Such food sources tend to be consistent while people are using recreation areas (Gehrt 2004; Bozek et al. 2007); however, raccoons depending on such resources tend to experience significant weight loss in the winter when less food is available (Prange et al. 2003), similar to winter stress effects documented elsewhere (Folk et al. 1968). Declining burdens from January to June may be explained by the nutritional stress on the raccoon host. Consequently, the shift from decreasing to increasing *B. procyonis* burdens that occurs in July may be in response to increased food resources associated with the increased human use of recreational areas. As raccoons aggregate to forage on refuse, there is increased contact among raccoons and likely

more contact with *B. procyonis* (Gompper and Wright 2005), which is especially important for infection in juvenile raccoons.

We provide support for Kazacos' (2001) assertion that the parasite population goes through a yearly cycle. The age structure of *B. procyonis* shifted throughout the year reflecting previously noted seasonal changes in prevalence. Worms attained their largest size in October and average worm length decreased from October through January. This shift to smaller worms (younger population) coincided with decreases in worm population size from January to June and provides evidence for a winter self-cure (Kazacos 2001). Reinfection of raccoons with *B. procyonis* in late spring and summer (Kazacos 2001) would explain the increasing worm lengths observed between January and October. It is likely that more susceptible young raccoons in the population play an important role in this increase, although there was only weak evidence of this in our data, perhaps related to overall age distributions in our sample. In addition, the fluctuations and self-cure we saw in our study may vary or not occur in other raccoon populations, such as those in the South not exposed to winter stress; this would be interesting to investigate.

Parasite populations tend to be fragmented as aggregates of individuals share a host. They are overdispersed because not all potential hosts are infected, and parasites are not distributed evenly (or randomly) across hosts (Anderson and May 1978). In fact, most hosts only have a few parasites and only a few hosts have high-intensity infections. This was true for our study, as only 7% of the infected animals had >50 worms. Populations of *B. procyonis* were biased toward females in this study. Female-biased sex ratios are common among parasitic nematodes, and may be influenced by many factors, including intensity of infections (Poulin 1997). We found increasingly female-biased populations; as burden decreased, the adult female population increased. This is consistent with trends observed in other nematode species (Poulin 1997; Rishniw et al. 2012). Several suggestions

have been made to explain this bias, including competition for females by males at low densities and differential longevity of females (Poulin 1997). In our study, we did not observe seasonal differences in the percentage of females and thus we cannot support the assertion of differential longevity of females. Increased competition for females by males in low-intensity infections is a reasonable explanation, but we do not have supporting evidence. It may simply be a matter that having more females is more beneficial for overall population success (based on egg production and thus transmission) and, based on multiple mating, 1:1 ratios of males:females are not necessary.

We provided evidence that *B. procyonis* undergoes a yearly fluctuation in population structure and worm numbers, and supports the presence of a self-cure in winter in temperate regions (Kazacos 2001), due to a loss of older, larger worms. Worm burdens and size then increased through summer and fall, related to recruitment of the parasite into the population, likely occurring primarily in juvenile raccoons. This helps explain the increasing prevalence over the year, which peaks in the fall as seen in various studies (Page et al. 2005). Using these data and the fact that latrines pose a risk to people visiting or living in close proximity to these locations, mitigation strategies may be developed and timed optimally to target peak populations of the parasite to best limit latrine contamination and potential transmission (Page et al. 2014). The apparent dependence of raccoons on anthropogenic food sources, such as garbage, at these locations may facilitate mitigation using medicated baits (Page et al. 2014) because these locations provide an excellent target for automated bait systems that deliver the baits routinely (Smyser et al. 2015b).

ACKNOWLEDGMENTS

We acknowledge the support of the Wheaton College Alumni Association, the Aldeen Fund, and the Science Division. We also appreciate the support of the Max McGraw Wildlife Foundation and the Forest Preserve District of Cook County.

We also acknowledge the assistance of Chuck Rizzo, Mike Neri, and Andy Burmesch of the Forest Preserve District of Cook County; Hannah O'Malley, Kenneth Delahunt, Steven Fazekas, Matthew Goode, and Lucas Bridges of the US Department of Agriculture; and numerous Wheaton College students for assistance with necropsies.

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Received for publication 11 June 2015.

Accepted 30 September 2015.