

**Gapeworm (*Syngamus trachea*) Infection in
First-Year European
Starlings (*Sturnus vulgaris*)
from Urban Airports in
Northeastern USA**

Zhuoxue Chen and Suzanne C. Sukhdeo



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Cover Photograph: Male and female gapeworms attached together. Photo by Suzanne Sukhdeo at the Sukhdeo Lab.

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Gapeworm (*Syngamus trachea*) Infection in First-Year European Starlings (*Sturnus vulgaris*) from Urban Airports in Northeastern USA

Zhuoxue Chen^{1*} and Suzanne C. Sukhdeo²

Abstract. First-year fledgling *Sturnus vulgaris* (European Starlings) (n = 773) were trapped from May to September in 2018 and 2019 at four local airports (EWR, TEB, JFK, and LGA) in the northeast USA. Overall, these birds had significant infections with the parasite *Syngamus trachea* (Gapeworm). In 2018, the mean prevalence of infection was 42.7%, and in 2019 the mean prevalence was 59.1%. The results suggest that rainfall was an important factor both in the levels of infection and in the seasonality of infections in these birds. This was most likely mediated by the effects of rainfall on earthworm behavior (the intermediate host carrying the infective larvae of these parasites). There was a strong negative correlation between the size of the bursa of Fabricius and infection levels of the parasites, with smaller bursae occurring in the birds with heavier infections.

Introduction

Syngamus trachea M. (Gapeworm) are parasitic nematodes that infect birds' tracheas and cause respiratory distress by clotting their airways (Akand et al. 2020). The parasite causes coughing, wheezing and open-mouthed breathing called gaping. Since the first public record of gapeworm-caused disease in 1797 by Wiesenthal (Wiesenthal 1797), we know that gapeworm has thrived in wild birds and poultry for more than two hundred years. *Sturnus vulgaris* L. (European Starlings) have been an invasive species in North America since the 1890s, and they are highly attached to urban settings (Belinsky et al. 2019). Starlings have a broad diet range, and their preferences for invertebrates and insect larvae during nesting season (Linz et al. 2018) make them good hosts for this parasite. Infection can occur when the birds feed on the encysted parasite larvae in their own feces (rare); typically, however, infections come from ingesting larval stages in earthworm intermediate hosts (Clapham 1934). The parasite has low host specificity and is known to infect both wild and domestic bird species, including European Starlings. This has long raised concerns for potential epizootic problems (Campbell 1935, Lewis 1925). Starlings are considered to be good reservoirs for the parasite and easily transmit gapeworms to local birds (Valente et al. 2014). Small open backyard poultry operations, or free-range chicken and turkeys, might have more contact with wild birds and face higher potential risks of infection (Akand et al. 2020, Carrisosa et al. 2021).

The population dynamics of parasites in avian hosts have been poorly investigated, primarily because of the difficulties in getting collection permits. The current study was made possible because invasive species like the European Starling are routinely depredated at local airports in an effort to reduce bird-aircraft collisions, and the carcasses are available to museums and universities. The purpose of this study was to investigate gapeworm infections in European Starlings from four local airports. Our findings indicate the presence

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of seasonal patterns in parasite prevalence and infection levels, highlighting the potential significance of rainfall as an important abiotic factor influencing gapeworm infection dynamics.

Materials and Methods

Sample collections

From May to September in 2018 and 2019, a total of 773 first-year fledgling *Sturnus vulgaris* (European Starlings) were captured at four local airports in the Northeast USA; Newark Liberty International Airport (EWR), Teterboro Airport (TEB), John F. Kennedy International Airport (JFK), and La Guardia Airport (LGA). US Fish & Wildlife Service (FWS) routinely depredates birds at airports to reduce bird/aircraft collisions. Starlings were trapped, euthanized, and frozen by FWS. Sample sizes and sampling times varied between airports because FWS officials at each airport were trapping birds on different schedules.

Necropsy

Starling carcasses were frozen when collected from FWS and kept frozen (-20°C freezer) until necropsy was performed, at which time they were thawed in warm water. The dates of capture and necropsy were recorded, and 8 bird metrics were collected: total body length, head length (including beak), right wing length, tail feather length, bird weight, and the weights of proventriculus and gizzard, spleen, and Bursa of Fabricius. Bird body lengths (bill-to-tail length) were measured in thawed birds by laying the bird on its back, flattening the head, and measuring from tip of bill to tip of the tail. The right wing of each bird was measured by gently flattening the wing and measuring the maximum length. Tail feather length was measured from the base of the tail to the longest feather length. For the necropsy, an incision was made from the bottom of the sternum to the base of the beak. The trachea was cut and separated from the gastrointestinal tract at the trachea-crop junction. A longitudinal incision was made along the entire length of the trachea and examined for gapeworms, which are large, red, and easily visible. Gapeworms were carefully removed and counted. The majority of gapeworms recovered were mature, but occasionally immature gapeworms were found and noted.

Temperature and rainfall data

Average monthly temperatures and rainfall data was collected from the Weather Underground site (Weather Underground 2022). For EWR, JFK and LGA, average temperature and rainfall were collected from each airport site. However, TEB (Teterboro Airport) did not have its own weather station, so the data for TEB is from the city of Teterboro. For rainfall model simulation, the rainfall data were derived from CHIRPS Precipitation Data available on NOAA's Environmental Research Division Data Access Program (ERDDAP) website (Simons 2022), the time resolution is 5 days, and the unit of rainfall level is in mm.

Data analysis

Intensity denotes the abundance of worms in a bird, and mean intensity was calculated as the mean number of parasites within infected birds in a sample. Infection is defined as the presence of parasites in the host, and intensity and prevalence (the percentage of the population infected), are key indicators used in parasitological studies to assess parasite population dynamics.

Welch's t-test was used to test differences between the two collection years for gapeworm infection, bird weight, bursa weight, and spleen weight. We used Pearson's product-moment correlation test to measure the correlation between each bird metric and gapeworm abundance (gapeworms per bird). To investigate the difference in parasite infection between two years while controlling for the potential effects of sampling location and month, we considered factors that could have influenced the observed differences. For instance, the variation could have been due to sampling a higher number of birds during months when the prevalence of gapeworm infection was higher in 2019. Additionally, it could have been influenced by sampling more birds from populations with a higher prevalence of the parasite in 2019. To address these considerations, we fitted a generalized linear mixed-effects model (GLMM) with negative binomial distribution (`glmer.nb`) in the `lme4` package (Bates et al. 2015), treating the number of parasites as the count response variable. We included sample month and location (specifically, the airport) as random factors to account for their potential impact. The year was treated as a fixed factor in the analysis. By incorporating these factors into the model, we aimed to mitigate any confounding effects and obtain a more accurate understanding of the differences in parasite infection between the two years. We also examined the impact of rainfall levels on parasite abundance by fitting a GLMM with negative binomial distribution. The GLMM included the rainfall level 20 days prior to the bird collection date as the explanatory variable, while the response variable was the abundance of gapeworm infection. Additionally, we accounted for the potential effects of airports of bird collection by setting it as random effects in the model.

To understand the correlation between parasite infection and bird immune system, GLMM with negative binomial distribution were fitted by using bird weight, bursa, or spleen weight (g) as explanatory variable and gapeworm abundance as response variable; month and airports of bird collection were set as the random effects. To avoid the effect of bird weight on bursa and spleen size, we used the ratio between bursa or spleen weight, and bird weight, to run the GLMM model. Analyses were performed in R Version 4.2.2 (R Core Team 2022) using the package "DHARMA" (Hartig 2018).

Results

First-year fledgling European Starlings ($n = 773$) were trapped from May–September in 2018 and 2019 at four local airports (EWR, TEB, JFK and LGA) in the northeast USA. Overall, in 2018, the mean intensity (number of parasites in an individual bird) of gapeworms was 1.82 (range: 1–14), and the mean prevalence (percent of population infected) was 42.7%. Infection levels were higher in 2019 with mean intensity of gapeworm at 2.86 (range: 1–15), and the mean prevalence was 59.1%. Gapeworm abundance in 2018 was significantly lower than infections in 2019 (Welch's t-test: $t = 6.95$, $P = 8.59e-12$; Fig. 1). The GLMM model, which controlled for sampling location and month, supported this finding by revealing a significant correlation between year and gapeworm abundance ($coefficient = 0.7118$, $SE = 0.1086$, $z\text{-value} = 6.557$, $p\text{-value} = 5.48e-11$). Gapeworm abundance varied over the season, and June and July counts from both years showed the highest gapeworm prevalence and intensity values at all four airports (Table 1). In 2018, gapeworm prevalence reached its peak in July (52.1%) and June had the highest gapeworm intensity (2.24; range: 1–14). In 2019, the peak prevalence (81.3%) and intensity (3.64; range: 1–8) occurred in July (Fig. 1).

According to the Pearson's product-moment correlation test, no significant correlations were found between infection level and most of the metrics collected in this study (bird

weight: $r(757) = 0.0214, p = 0.556$; wing length: $r(614) = 0.0432, p = 0.285$; head-beak length: $r(610) = -0.0416, p = 0.304$; intestine length: $r(730) = 0.0553, p = 0.135$; gizzard weight: $r(742) = -0.0475, p = 0.195$). Although the bird body length was significantly correlated with the infection level, the Pearson correlation coefficient did not show a strong negative correlation ($r(755) = -0.0860, p = 0.0180$). There were no significant differences between bird weights in 2018 and 2019 (Welch's t -test: $t = 0.968, P = 0.334$). The mean weight for the starlings in 2018 was 65.4 ± 0.42 g, and the mean weight in 2019 was 65.9 ± 0.40 g. The spleen weight did not show significant difference between the two years (Welch's t -test: $t = 0.539, P = 0.590$). The mean spleen weight was 0.165 ± 0.011 g in 2018 and 0.171 ± 0.005 g in 2019. Differences between mean bursa weight for 2018 and 2019 are significant (Welch's t -test: $t = 2.75, P = 0.00622$). The mean bursa weights were 0.131 ± 0.005 g and 0.147 ± 0.003 g in 2018 and 2019, respectively.

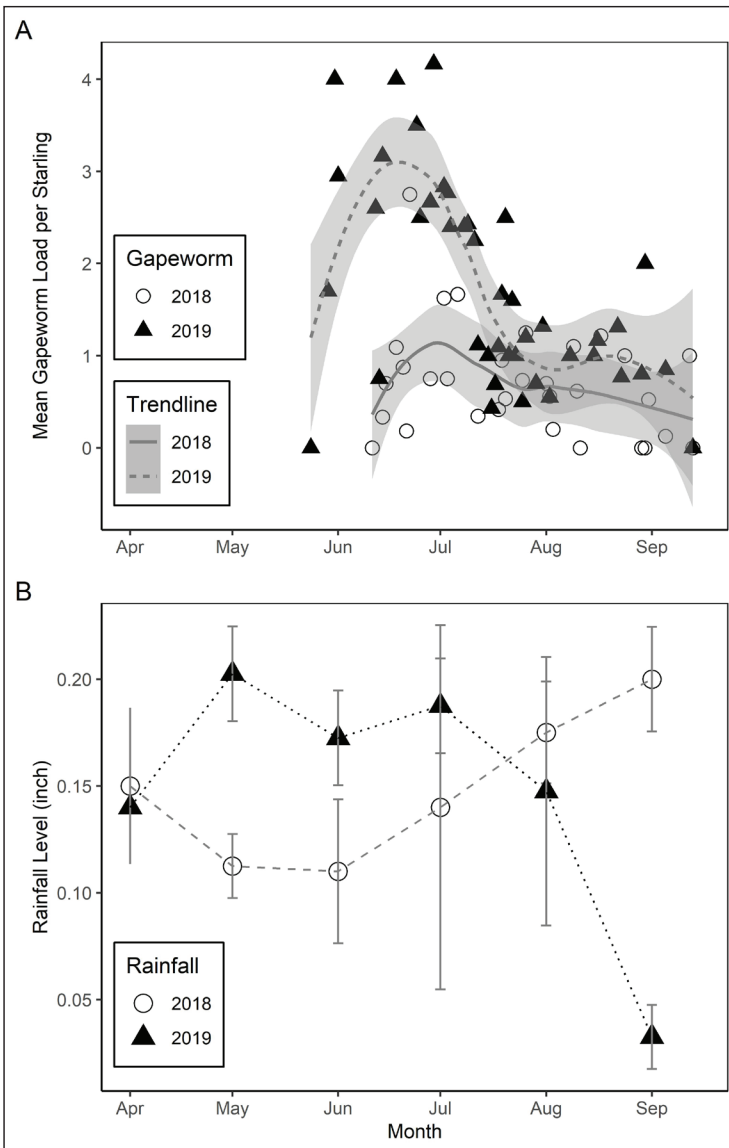


Figure 1. Comparisons between rainfall level and gapeworm infections in 2018 and 2019. A. Gapeworm infection levels for 2018 and 2019. B. Mean monthly rainfall levels for 4 airports. Rainfall data are derived from airport weather stations.

Table 1. Number of starlings caught in each airport, monthly gapeworm intensity and prevalence in 2018 and 2019 from four airports.

Month Year	EWR			JFK			LGA			TEB		
	# of birds	Intensity	Prevalence	# of birds	Intensity	Prevalence	# of birds	Intensity	Prevalence	# of birds	Intensity	Prevalence
June 2018	42	1.44	38%	23	2.18	48%	0	-	-	16	4.14	44%
July 2018	35	1.50	23%	28	2.13	54%	53	1.34	72%	30	1.67	50%
August 2018	13	1.00	8%	33	2.25	36%	38	1.85	34%	29	1.79	48%
September 2018	16	1.50	13%	0	-	-	0	-	-	0	-	-
May 2019	16	3.30	63%	0	-	-	0	-	-	0	-	-
June 2019	30	3.43	70%	40	4.09	83%	21	3.10	95%	0	-	-
July 2019	35	2.47	43%	42	2.83	69%	40	2.54	60%	40	3.29	53%
August 2019	36	1.88	44%	40	2.36	35%	13	3.33	46%	29	1.67	62%
September 2019	0	-	-	1	-	0%	0	-	-	20	1.55	55%

Two linear models suggested significant effects between bird weight and spleen and bursa size (p -value: bursa: $< 2.20e-16$; spleen: $< 2.20e-16$). This indicated the possible effects of bird weight and thus the bursa (spleen) and body weight ratio were used to run the gapeworm infection model. The bursa GLMM model showed a significant negative correlation between bursa weight and gapeworm infection, with smaller bursae occurring in the birds with heavier infections ($coefficient = -11.27, SE = 4.99, z\text{-value} = -2.258, p\text{-value} = 0.0240$; Fig. 2). No significant correlation between the gapeworm infection and spleen weight was detected ($coefficient = -5.74, SE = 3.53, z\text{-value} = -1.628, p\text{-value} = 0.1036$; Fig. 3), but we can still observe a negative relationship with the model prediction. The GLMM model for rainfall level suggested that the rainfall can be a potential factor which influences the gapeworm abundance ($coefficient = 0.009489, SE = 0.004061, z\text{-value} = 2.337, p\text{-value} = 0.0194$; Fig. 4). Our evaluation of the model's fit using the DHARMA package revealed no alerts or discrepancies, indicating a good fit of the statistical model to the data. The QQ plot displayed a diagonal line, suggesting that the observed quantiles closely matched the expected quantiles under the assumed distribution. Additionally, the Residuals vs. Predicted plot demonstrated a random scatter of residuals around zero, indicating no systematic patterns or deviations. These findings provide evidence for the adequacy of our model in capturing the underlying relationships within the data.

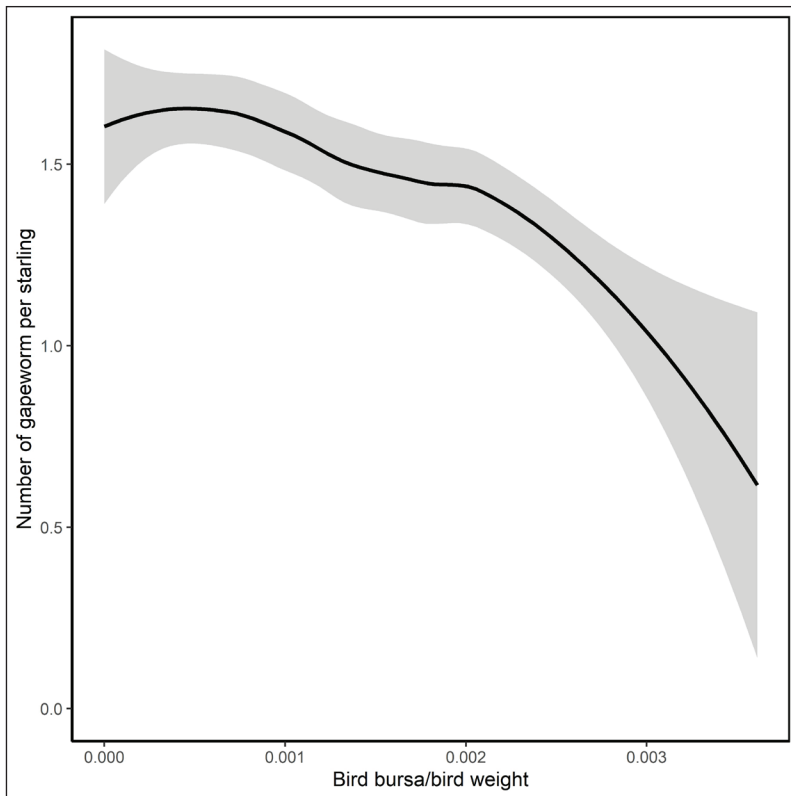


Figure 2. Relationship between gapeworm abundance and the ratio between bursa of Fabricius and bird weight. The model was fitted by using combined 2019 and 2018 data, and it shows the significant negative correlation between bursa weight and gapeworm infection. The trendline used a loess regression the confidence interval is grey.

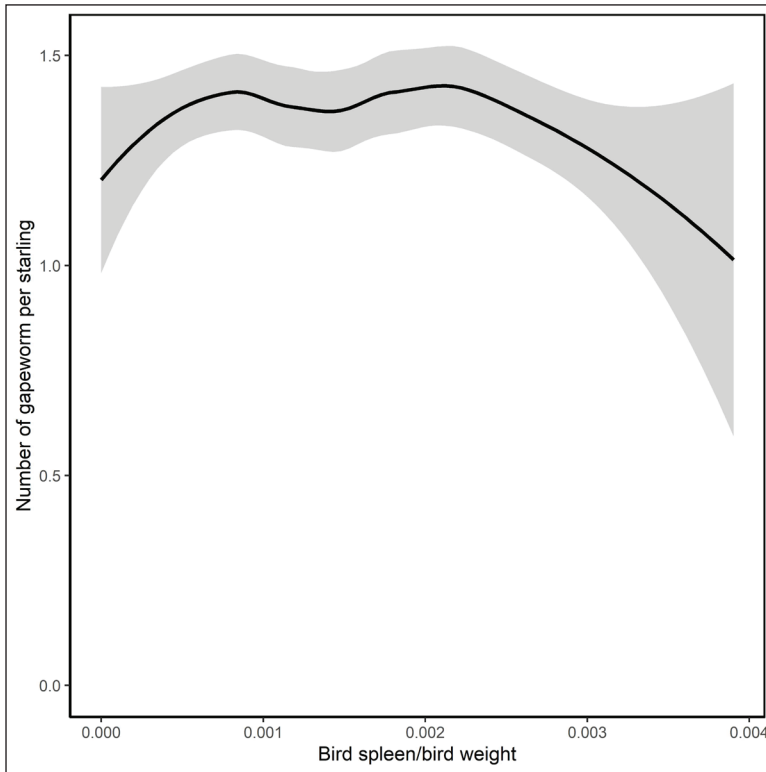


Figure 3. Relationship between gapeworm abundance and the ratio between spleen and bird weight. The model was fitted by using combined 2019 and 2018 data, and it shows the negative correlation between bursa weight and gapeworm infection. The trendline used a loess regression and the confidence interval is grey.

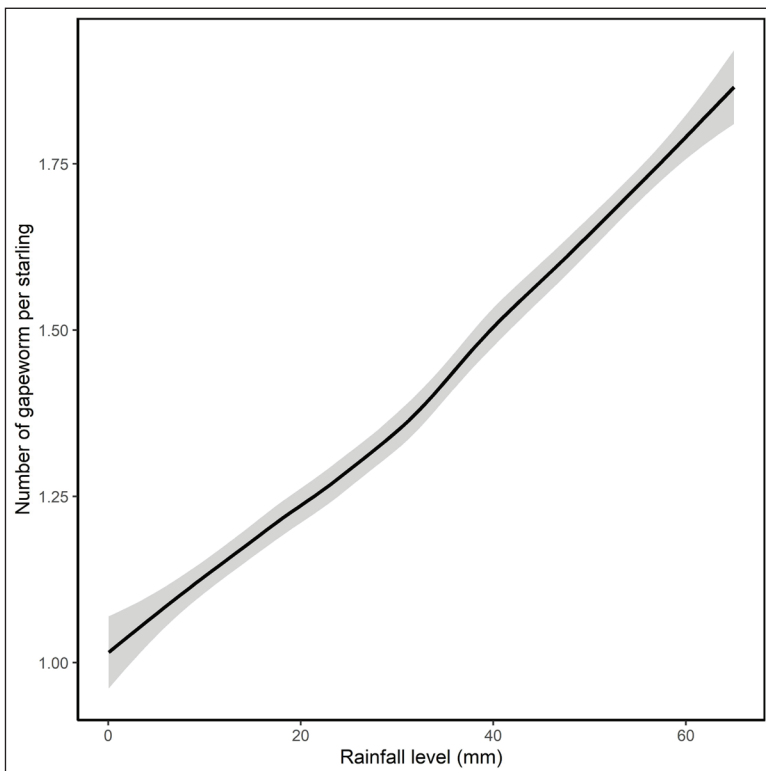


Figure 4. Relationship between gapeworm abundance and rainfall level 20 days prior to the bird collection date. The model was fitted by using combined 2019 and 2018 data, and it shows the positive correlation between rainfall level and gapeworm infection. The trendline used a loess regression and the confidence interval is grey.

Discussion

The results of this study indicate that wild-caught starlings in the Northeast US have significant infections with gapeworm parasites. Infection prevalence was as high as 95% in some samples, and with up to 4 worm pairs recovered from a single bird. Infections varied greatly across months, and there were significant differences in prevalence and infection intensity between 2018 and 2019. The data suggests that differences in parasite infection levels between the collection years might have been driven by differences in rainfall, and much less by differences in average temperatures between the two years. While no correlations were found between infection level and most of the metrics collected in this study (weight, size, organ weights), analysis reveals that there was a negative correlation between the size of the bursa of Fabricius and infection level of the parasites, with smaller bursae occurring in the birds with heavier infections.

The size of the Bursa of Fabricius is often used as a proxy for the immune response in birds (Møller et al. 1996, 1998). This study found that starlings with higher infection levels tended to have smaller bursae. The significance of this finding is not clear because the effects of parasites on the size of the bursa are still being debated. In some ectoparasite studies, bursal size was negatively associated with elevated parasite infections (Stenkewitz et al. 2014). However, infections with protozoan parasites like *Eimeria tenella* T. can have the opposite effect and result in an increase in bursal size (Zhou et al. 2015). The bursa is an important part of the immune response to pathogens because it is a central lymphoid organ, required for development of the antigen-specific B cell repertoire (Glick 1983). The size of the bursa reflects its cell population, and thus its antibody production (Roulin et al. 2001). Although in commercial operations, the Bursal-Body index (BB index) is a tool to assess the health status of chickens (Raji et al. 2017), bursal size as a correlate of parasite infections may not be an appropriate metric. In chickens, inter-individual differences occur in the size of this organ because bursal size is influenced by many factors including sex, breed, rearing conditions, age, disease and parasitism (Cazaban et al 2015). The immune role of bursa is primarily important for young birds (Glick 1983) and may be indicating a strong response to infection in our sample, but these data can only be taken as suggestive on the role of the bursa in gapeworm infections.

Our results suggest that rainfall can be an important factor that contributes to seasonal gapeworm infection by influencing earthworm behavior. We used several statistical models to explore the population dynamics of gapeworms and eliminate potential factors influencing their abundance. The GLMM model indicates a significant correlation between year and gapeworm abundance, suggesting variations in gapeworm abundance in 2018 and 2019. Furthermore, the GLMM model for rainfall suggested that rainfall could potentially influence gapeworm abundance. The evaluation of the model's fit indicated a good match between the observed and expected quantiles, with no systematic patterns or deviations in the residuals. These findings provide evidence supporting the adequacy of the model in capturing the underlying relationships within the data and support the notion that rainfall was related to parasite infection. A previous study reported that temperature and humidity were both positively associated with gapeworm larval abundance in soil, but concluded that rainfall had very little effect (Gething et al. 2015). However, the indirect effects of rainfall via the earthworm intermediate host may be more important in transmission than larval abundance. Starlings are primarily infected by ingesting larval stages of the parasite contained inside infected earthworms, and rarely get infected directly from ingesting larvae in the soil (Clapham 1934). Earthworms exchange gases through their skins, and this is one

explanation why rain brings earthworms to the surface where they are more easily predated on by the birds (Onrust et al. 2019). Thus, rain can influence the encounter rates between infective earthworms and starlings. It is notable that just like starlings, a large number of earthworm species in North America are also invaders from Europe (James and Hendrix 2004, Linz et al. 2007), and the parasite life cycle is well-adapted to the biology of these two hosts. In sparrows, parasites tend to be more prevalent in yearling birds than full adults (Holand et al. 2013). The birds in our study were yearlings and yearlings tend to prefer invertebrates like earthworms and some insect larvae (Linz et al. 2018). If infection levels are related to rainfall via the effects on earthworm behavior, it follows that the seasonal patterns of rainfall will also predict the seasonal variation in levels of parasite infections in the birds, as was observed.

From a practical point of view, the high levels of parasite infection in these wild birds suggest that an important consideration might be potential epizootics. This parasite has low host specificity, and infections in wild European Starlings have long raised the concern for epizootics (Campbell 1935, Lewis 1925). Backyard poultry farming is increasing in urban settings in the United States (Cadmus et al. 2019, Elkhoraibi et al. 2014, Pollock et al. 2012), and wild birds like starlings which are highly attached to urban settings will increase the transmission rate of gapeworm and other avian parasites.

In summary, this study demonstrates that infections with the nematode gapeworm parasite *Syngamus trachea* are endemic and highly prevalent in wild-caught starlings in northeast USA. The data suggests that rainfall may be an important abiotic factor in bird infections, probably through the higher availability of earthworm intermediate hosts during periods of high rainfall. It should be noted that there are some limitations regarding our analyses. Sample sizes were uneven because of the dependence on US Fish & Wildlife Service to collect the samples, and it may require greater than two years of data to more accurately define the relationship between rainfall and gapeworm infection.

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