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ABSTRACT: Avian trichomonosis, caused by the protozoan *Trichomonas gallinae*, affects bird-eating raptors worldwide. Raptors can develop trichomonosis by feeding on infected prey, particularly Rock Pigeons (*Columba livia*), which are a reservoir for *T. gallinae*. Raptors may be particularly vulnerable to *T. gallinae* infection in degraded habitats, where changes in resources may cause raptors to switch from foraging on native prey to synanthropic avian species such as Rock Pigeons. Golden Eagles (*Aquila chrysaetos*) typically forage on mammals; however, habitat across much of their range is experiencing degradation through changes in land use, climate, and human encroachment. In 2015, we examined the prevalence of *T. gallinae* infection in Golden Eagle nestlings across western North America and conducted an intensive study on factors associated with *T. gallinae* infection and trichomonosis in southwestern Idaho. We found *T. gallinae* infection in 13% (12/96) of eagle nestlings across 10 western states and in 41% (13/32) of nestlings in southwestern Idaho. At the Idaho site, the probability of *T. gallinae* infection increased as the proportion of Rock Pigeons in nestling diet increased. Nestlings with diets that consisted of ≥10% Rock Pigeons had a very high probability of *T. gallinae* infection. We compared historical (1971–81) and recent (2014–15) diet data and incidence of trichomonosis lesions of nestling eagles in Idaho and found that the proportion of Rock Pigeons in eagle diets was higher in recent versus historical periods, as was the proportion of eagle nestlings with trichomonosis lesions. Our results suggested that localized shifts in eagle diet that result from habitat degradation and loss of historical prey resources have the potential to affect Golden Eagle nestling survival and supported the hypothesis that land use change can alter biologic communities in a way that might have consequences for disease infection and host susceptibility.

Key words: Diet shift, disease, raptor, Rock Pigeon.

INTRODUCTION

Avian trichomonosis, caused by the flagellated protozoan parasite *Trichomonas gallinae*, is an infectious disease affecting avian communities worldwide (Tompkins et al. 2015). *Trichomonas gallinae* is commonly found in birds in the Columbidae family, and the parasite has followed the introductions, and range expansions, of Rock Pigeons (*Columba livia*) worldwide (Stabler 1947). *Trichomonas gallinae* primarily affects the upper digestive tract of birds, where it can cause the development of caseous lesions in the oropharynx that can lead to starvation or suffocation (Amin et al. 2014). Previously unexposed avian populations can be severely affected by the parasite (Bunbury et al. 2008), and significant population declines of common avian species from *T. gallinae* exposure (Robinson et al. 2010) suggest that populations of rare or threatened species that are

naïve to *T. gallinae* infection may be vulnerable.

Bird-eating raptors that feed on *T. gallinae*-infected prey are susceptible to infection and the development of trichomonosis that often results in mortality. Previous studies found high rates of trichomonosis in raptors where loss of native habitat and prey resulted in dietary shifts. Bonelli's Eagles (*Aquila fasciata*) in northeastern Spain increase their consumption of Rock Pigeons as preferred prey populations decline, increasing the risk of *T. gallinae* infection and becoming a major cause of nestling mortality (Real et al. 2000; Palma et al. 2006). Similar studies describe high *T. gallinae* infection rates in local populations of Cooper's Hawks (*Accipiter cooperii*) in Arizona (Boal et al. 1998) and Northern Goshawks (*Accipiter gentilis*) in Great Britain (Cooper and Petty 1988) and Poland (Wieliczko et al. 2003), where landscape-level changes and human development cause shifts in diets toward higher proportions of synanthropic columbids. In addition to diet, oral pH may affect risk of *T. gallinae* infection. *Trichomonas gallinae* persists at a pH range of 6.5–7.5 (Read 1957) but is less viable in more-acidic conditions. Oral pH of nestling Cooper's Hawks creates a hospitable environment for *T. gallinae*, but oral pH decreases as hawks age, and adults are less susceptible to infection (Urban and Mannan 2014). Differential susceptibility in Cooper's Hawks based on age groups suggests differences in oral pH could affect susceptibility to *T. gallinae* infection within individuals.

In western North America, Golden Eagles (*Aquila chrysaetos*) occupy open habitats, including shrub steppe ecosystems, and prey primarily on rabbits and hares (Leporidae) and ground squirrels (Sciuridae; Bedrosian et al. 2017). Over the last century, anthropogenic actions have degraded and fragmented shrub steppe ecosystems (Leu et al. 2008), which could have affected trophic interactions. For example, Golden Eagles in the sagebrush steppe of southwestern Idaho historically preyed on black-tailed jackrabbits (*Lepus californicus*; Steenhof and Kochert 1988). Since the early 1980s, the native shrub communities that support jackrabbits have been reduced through the effects of wildfire, invasive plants, and land development (Kochert et al. 1999). These landscape-level changes have been associated with significant shifts in Golden Eagle diets, with a decrease in the proportion of jackrabbits and an increase in avian prey, including Rock Pigeons (Heath and Kochert 2016).

Given the changes to western North American landscapes that have altered prey availability for Golden Eagles (Bedrosian et al. 2017), and increased contact with synanthropic species like Rock Pigeons, our objectives were to document the prevalence of *T. gallinae* in nestling Golden Eagles, identify the factors associated with infection, and examine whether infection risk has changed over time. We sampled Golden Eagle nestlings throughout western North America during the 2015 breeding season to assess the geographic prevalence of *T. gallinae* infection. In addition, we conducted an intensive study in southwestern Idaho to examine whether nestling age, oral pH, or proportion of Rock Pigeons in nestling diet predicted *T. gallinae* infection rates. Finally, we used historical (1971–81) and recent (2014–15) data to examine how nestling diet and incidence of trichomonosis have changed over time at our Idaho study site.

MATERIALS AND METHODS

Prevalence of *T. gallinae* in western North America

From April to June 2015, we visited historical Golden Eagle nesting territories at 11 study sites in western North America to examine nestlings and collect oral swab samples (Fig. 1). At sites outside of Idaho, we made one or two visits to nests to examine all nestlings and collect swabs (n=123) when nestlings were approximately 28 and 56 d old. At the intensive study site in Idaho, in the Morley Nelson Snake River Birds of Prey National Conservation Area (NCA) and the adjacent upstream comparison area (42°50′N, 115°50′W), we visited nests every 8–10 d during the nestling period, resulting in three or four repeated swab samples per nestling (n=122 swabs). We entered eagle nests when we estimated nestlings to be old enough to thermoregulate, approximately 21 d old (Kochert et al. 2002).

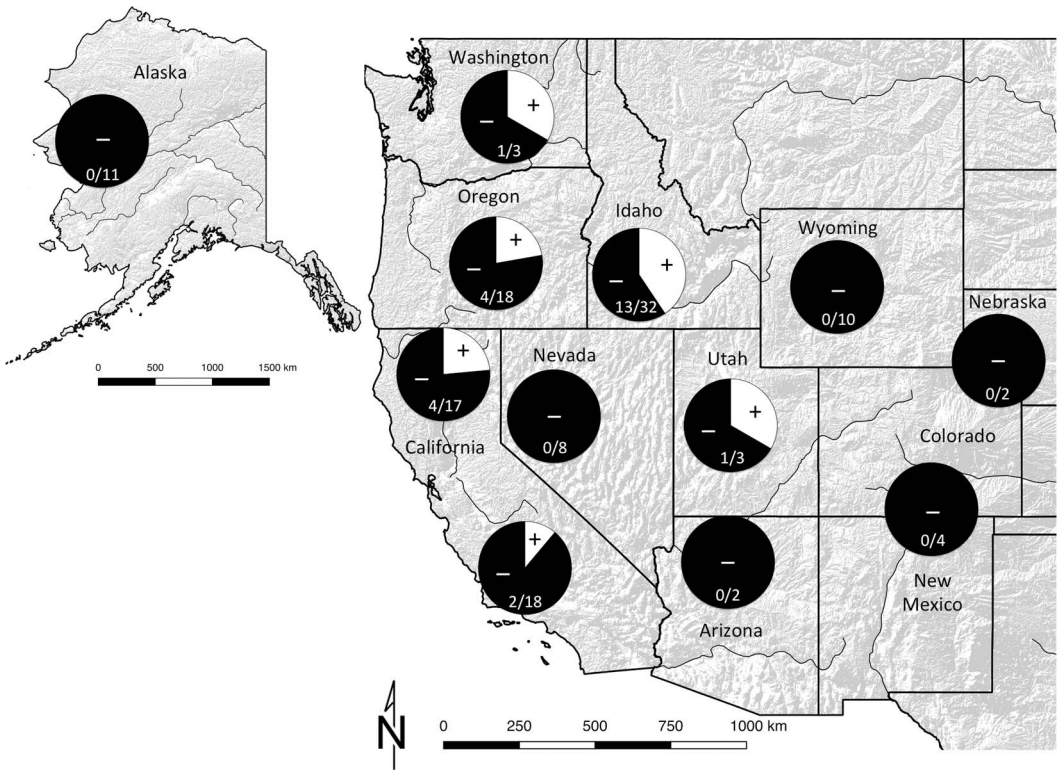

FIGURE 1. Location of study sites where oral swabs were collected from Golden Eagle (*Aquila chrysaetos*) nestlings to test for *Trichomonas gallinae* in the western USA from April–June 2015. Pie charts represent distinct sampling sites. Proportions in each pie chart show the number of nestlings that tested positive in culture for *T. gallinae* out of the total nestlings sampled at each site.

Once in the nest, we assessed nestling age to the nearest day based on criteria from Hoechlin (1976).

We swabbed the surfaces of the nestling's mouth and oropharynx with a dry, cotton-tipped swab to sample for *T. gallinae*. Swabs were immediately introduced into culture medium in InPouch TF *Tritrichomonas foetus* test kits (BioMed Diagnostics, White River, Oregon, USA). Samples collected in Idaho were incubated at 37 C for 24 h, within 24 h of collection. Samples collected outside of Idaho were shipped overnight to Boise State University (Heath Laboratory, Boise, Idaho) and incubated in the same conditions within 72 h of collection. A delayed start to incubation did not affect our ability to detect the presence of *T. gallinae* in a trial study with four duplicate samples undergoing 24-, 48-, and 72-h delays until incubation (B.M.D. unpubl. data). After initial incubation, we examined InPouch kits using a compound light microscope at 100× magnification (Cover et al. 1994) every 24 h. We identified *T. gallinae* by morphologic characteristics (Stabler 1947). If no motile trichomonads were detected within 144 h of initial incubation, samples were considered negative for *T. gallinae* (BioMed Diagnostics 2012).

We performed DNA extractions on 17 InPouch kits to confirm the presence of *T. gallinae*, identify the strain, and test for false negatives (Table 1). Additionally, DNA extractions were performed on eight samples collected in Oregon and Utah that were not incubated within 72 h but were suspected to contain *T. gallinae* based on the observation of oral lesions or Rock Pigeon remains in the nest. We performed PCR amplification and sequencing of the ITS1-5.8S-ITS2 ribosomal region using the primers described in Cepicka et al. (2005). Forward and reverse sequences were assembled and aligned, and consensus sequence chromatograms were trimmed and edited by hand using Sequencher 5.3 (Gene Codes Corporation, Ann Arbor, Michigan, USA). The resultant nucleotide sequences were subjected to BLAST (National Center for Biotechnology Information 2017).

In addition to swabs, we examined the mouth and oropharynx of eagle nestlings macroscopically

TABLE 1. Trichomonad molecular analysis results from oral swab samples from Golden Eagle (*Aquila chrysaetos*) nestlings in nine western North American study sites in 2015. Percent sequence identity reported to the closest GenBank acession utilizing BLASTn analysis.

Study site[a]	Culture results[b]	Consensus sequence obtained[c]	Culture and PCR agreement[d]	*Trichomonas* spp.		
				Trichomonas gallinae		*Trichomonas gypaetinii*
				KX584000[e]	LC136936[e]	KF993707[e]
AK	−	No	Yes	0	0	0
No. CA	+	Yes	Yes	100	0	0
No. CA	−	Yes	No	100	0	0
No. CA	−	Yes	No	100	0	0
No. CA	−	Yes	No	100	0	0
So. CA	+	Yes	Yes	0	0	100
So. CA	−	Yes	No	98	0	0
So. CA	−	Yes	No	0	100	0
ID	+	Yes	Yes	100	0	0
ID	+	Yes	Yes	100	0	0
ID	+	Yes	Yes	0	0	100
ID	+	Yes	Yes	0	0	100
ID	−	Yes	No	0	100	0
NM	−	No	Yes	0	0	0
OR	Unk	No	n/a	0	0	0
OR	Unk	Yes	n/a	99	0	0
OR	Unk	Yes	n/a	100	0	0
OR	Unk	No	n/a	0	0	0
OR	Unk	Yes	n/a	100	0	0
OR	Unk	Yes	n/a	100	0	0
OR	Unk	No	n/a	0	0	0
UT	Unk	Yes	n/a	99	0	0
UT	+	Yes	No	0	0	0
WA	−	Yes	No	100	0	0
WY	−	No	Yes	0	0	0

[a] Study site where nestling oral swab samples were collected: AK = Alaska; no. CA = northern California; so. CA = southern California; ID = Idaho; NM = New Mexico; OR = Oregon; UT = Utah; WA = Washington; WY = Wyoming.

[b] Results obtained via microscopy: + = sample containing *T. gallinae*; − = sample free of *T. gallinae*; Unk = unknown samples that were not incubated within 72 h but from nestlings potentially exposed to *T. gallinae* based on diet composition.

[c] Results obtained via PCR: yes = consensus sequence obtained from bidirectional sequences; no = no useable sequence could be obtained.

[d] Agreement between *T. gallinae* detection methods: yes = agreement between PCR and sequence results and microscopy results; no = PCR and sequence results and microscopy results did not agree; n/a = not applicable.

[e] Closest GenBank accession number.

for oral lesions. We considered immobile, caseous lesions indicators for trichomonosis. At the Idaho site, nestlings with oral lesions were treated with a 30-mg oral dose of carnidazole (Janssen Pharmaceutica, Beerse, Belgium), an antiprotozoal drug, after we collected an oral swab. We monitored treated nestlings for reinfection on subsequent visits. By treating nestlings with trichomonosis, we were able to prevent nestling mortality (J.A.H. unpubl. data), continue collecting diet data, and observe rates of reinfection. We did not include subsequent swabs from treated nestlings in our analysis of factors associated with *T. gallinae* infection.

Factors associated with *T. gallinae* infection

At the Idaho site, we took measurements of the oral pH of 15 eagle nestlings every 8–10 d throughout the nestling period. We held a microelectrode (Cole-Parmer, Combination pH Microelectrode BNC, Vernon Hills, Illinois, USA) under the ventral surface of the tongue until the reading on a digital field meter (Oakton, pH

Tester 10 BNC, Vernon Hills, Illinois, USA) stabilized. The microelectrode was stored in a 4.0 pH buffer solution (Aldon Corporation, Avon, New York, USA) during transport in the field and was rinsed with distilled water before use. We calibrated the microelectrode to three points (pH=4.0, 7.0, and 10.0) at least once a day prior to sampling (Urban and Mannan 2014). Although pH meters are sensitive and require sufficient moisture to operate properly, swabbing the oral cavity did not appear to affect the moisture level in nestlings' mouths. During the last visit, we collected blood using 27-ga needles and unheparinized collection tubes. We determined nestling sex through DNA analysis of blood samples at Purdue University (West Lafayette, Indiana, USA).

We sampled the diets of eagle nestlings by collecting prey remains and pellets (Steenhof and Kochert 1985; Heath and Kochert 2016) when we visited nests to swab and examine nestlings (21–56 d old). We tallied the frequency of all unique prey items collected from nests to calculate the proportion of Rock Pigeons in nestling diet.

Historical versus current diet composition and rates of trichomonosis

We used historical (1971–81) diet data (Steenhof and Kochert 1988) and diet data collected in 2014 and 2015 (Heath and Kochert 2016) to determine whether the proportion of Rock Pigeons in nestling diet had changed over time at the Idaho sites. For these comparisons, we only used data collected at 17 eagle territories sampled in both periods by the same method (prey remains and pellet analysis). In addition, we reviewed data from 1971–81 to document the frequency of oral lesions suggestive of trichomonosis (US Geological Survey Snake River Field Station unpubl. data). From 1971–81, technicians examined eagle nestlings including checking the mouth and oropharynx for caseous lesions. We compared the number of eagles with lesions and without lesions between the historical study and the 2015 season. All field methods followed protocols approved by the Boise State University Institutional Animal Care and Use Committee (Protocol 006-AC14-007).

Data analyses

We used generalized linear mixed models (GLMM) with presence and absence of *T. gallinae* (determined through culture) as a binomial response variable, and nestling- and territory-identity as random variables to account for nonindependence of samples, to assess factors associated with the *T. gallinae* infection. We used two separate models to evaluate whether nestling age or oral pH explained *T. gallinae* presence or absence. Also, we created a linear mixed model to examine whether oral pH changed with nestling age, sex, or an interaction between age and sex. Finally, we used a GLMM with presence and absence of *T. gallinae* as a binomial response variable and the proportion of Rock Pigeons in nestling diets as the predictor variable to test whether the proportion of Rock Pigeons in nestling diet predicted *T. gallinae* presence or absence.

To examine whether the proportion of Rock Pigeons as prey changed between the historical period (1971–81) and recent period (2014–15), we used a GLMM with a negative binomial distribution. The response variable was the total count of Rock Pigeon remains found in each nest in each year, and the predictor was binomial sample period (historical or recent) with an offset for the total prey items cataloged at each nest in each year. We used a GLMM with a binomial distribution with the presence or absence of oral lesions as the response variable to examine the interaction between study period (i.e., historical vs. recent) and the proportion of Rock Pigeons in the diet to determine whether the relationship between Rock Pigeon consumption and the probability of developing trichomonosis changed over time. Both models included territory identity as a random variable. All numeric predictors were scaled and centered before analysis. For GLMMs, we created confidence intervals by back-transforming the prediction after adding and removing the standard error. Linear models were created using function lmer, binomial models were created using function glmer (package lme4, Bates et al. 2015), and the negative binomial model was created using function glmmADMB (package glmmADMB, Fournier et al. 2012). All analyses were performed in R (version 3.2.2, R Development Core Team 2016). We considered $P \leq 0.05$ to be statistically significant. Descriptive statistics are reported as mean±SD. Proportions are presented as positive outcome/total sample.

RESULTS

We found the incidence of *T. gallinae* infection at six western North American study sites: northern California, southern California, Oregon, Utah, Washington, and Idaho (Fig. 1). Prevalence of *T. gallinae* in non-Idaho Golden Eagle nestlings was 13% (12/96), and 18% (11/62) of nests had at least one nestling that had a positive *T. gallinae* culture. In Idaho, the prevalence of *T. gallinae* infection was higher than at the other western sites; *T.*

gallinae was detected in 41% (13/32) of nestlings, and 42% (8/19) of nests had at least one nestling that had a positive *T. gallinae* culture. About 92% (12/13) of Idaho nestlings that had positive cultures for *T. gallinae* subsequently developed oral lesions suggestive of trichomonosis.

We confirmed the presence of *T. gallinae* with DNA extraction and DNA amplification via PCR in 64% (16/25) of samples (Table 1). Sequence analysis identified the presence of non-*T. gallinae* protozoans in four samples. Three isolates showed 100% identity and 100% coverage to *Trichomonas gypaetinii* (Martínez-Díaz et al. 2015). Additionally, one sequence had a 95% identity and 100% coverage to *Monocercomonas colubrurom*, a protozoan found in the intestines of reptiles (Richter et al. 2008). Our PCR and sequence results had a 53% (9/17) agreement to detection of a *Trichomonas* sp. via microscopic observations of culture samples. Using PCR and sequencing identified seven false negative samples, where *T. gallinae* was not detected through microscopy, and one false positive sample where *M. colubrurom* was misidentified as *T. gallinae*. In addition, PCR and sequencing detected *T. gallinae* in 50% (4/8) of samples from Oregon and Utah that were not incubated within 72 h of collection and where no living organisms were detected microscopically.

Mean nestling age when *T. gallinae* infection was detected in culture was 23.5±11.0 d (range 8–38 d). The mean age of oral lesion appearance was 30.3±13.5 d (range 12–49 d). We observed the development of lesions 7.2±7.0 d after detecting presence of *T. gallinae* in culture. In all cases in which we observed oral lesions and administered carnidazole, lesions disappeared within 8–10 d, and *T. gallinae* was not detected in cultured swabs on the subsequent visit. We observed *T. gallinae* reoccurrence in cultured samples, and reoccurrence of oral lesions, in 25% (3/12) of treated nestlings. Oral lesions reappeared within 16, 24, and 25 d of initial treatment. All nestlings were successfully retreated.

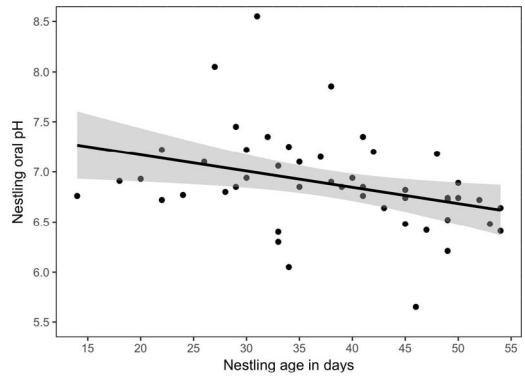

FIGURE 2. Observed oral pH (dark circles) and predicted line (dark line) with associated 95% confidence intervals (solid gray area) of Golden Eagle (*Aquila chrysaetos*) nestlings aged between 14–54 d old (n=15) sampled in southwestern Idaho, USA in 2015 as part of an investigation into the effect of *Trichomonas gallinae* on nestling infection and survival.

Nestling age did not predict the probability of *T. gallinae* infection (χ^2=0.3, n=32, P=0.58). Oral pH of nestlings decreased as nestlings aged (χ^2=9.0, n=15, P=0.003, Fig. 2) and was not related to nestling sex (χ^2=0.3, n=15, P=0.25). Mean oral pH of nestlings at least 49 d old was 6.68 (range 6.21–6.89). Although nestling oral pH decreased as nestlings aged, there was no significant relationship between *T. gallinae* infection and oral pH (χ^2=2.1, n=15, P=0.14).

We identified 749 unique prey items from eagle nests in 2015, 50 of which were Rock Pigeons (7%). The proportion of Rock Pigeon remains in nestling diets ranged from 0–0.39 per nest. The proportion of Rock Pigeons predicted *T. gallinae* infection (χ^2=4.5, n=32, P=0.03, Fig. 3). As the proportion of Rock Pigeons in the diet increased, so did the probability of developing *T. gallinae* infection; probability of infection approached one when Rock Pigeons accounted for ≥0.10 of nestling diet.

We found that the proportion of Rock Pigeons in the diet of Golden Eagle nestlings diet was higher in 2014–15 compared to 1971–81 (χ^2=7.9, n=155, P=0.005, Fig. 4). From 1971–81, 15% (31/213) of nestlings had oral lesions indicative of trichomonosis. An-

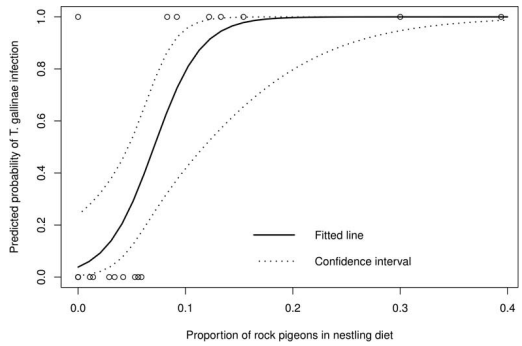

FIGURE 3. Observed occurrence (open circles) and predicted probability (solid line) with associated 95% confidence intervals (dotted lines) of *Trichomonas gallinae* infection in Golden Eagle (*Aquila chrysaetos*) nestlings (n=32) in relation to the proportion of Rock Pigeons (*Columba livia*) in the diet of nestlings in southwestern Idaho, USA in 2015.

nual rates ranged 0% (0/18) to 42% (11/26) compared to 41% (13/32) of nestlings in 2015. We did not find a significant interaction between the proportion of Rock Pigeons in the diet and sampling period on the probability of developing oral lesions, suggesting that probability of developing infection as a result of consuming Rock Pigeons did not differ between sampling periods (χ^2=1.2, n=155, P=0.26).

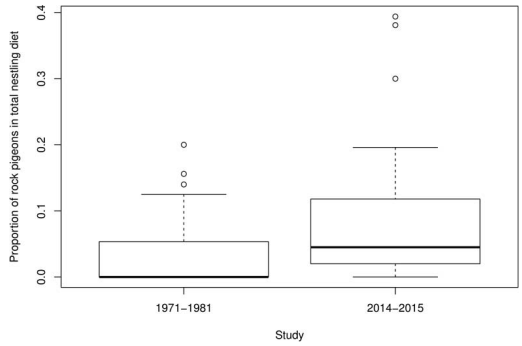

FIGURE 4. Proportion of Rock Pigeons (*Columba livia*) in Golden Eagle (*Aquila chrysaetos*) nestling diets in southwestern Idaho, USA at the same 17 territories during the historical period (1971–81, n=213) and the recent period (2014–15, n=32). Bold lines within boxes representing the median, upper, and lower limits of the box are the first and third quartiles, whiskers contain 1.5 times the interquartile range, and open circles are outliers.

DISCUSSION

Parasites such as *T. gallinae* reduce survival of nestling raptors and may become a conservation concern when landscape-level changes increase transmission and infection rates in raptor populations. We found evidence of *T. gallinae* infection in Golden Eagle nestlings in six western North American study sites, with a relatively high infection rate in southwestern Idaho. High infection rates in Idaho were associated with the proportion of Rock Pigeons in nestling diet, which has increased significantly compared to historical nestling diets (1971–81). Previous studies reported high mortality rates in nestling raptors that develop trichomonosis (100%, Cooper and Petty 1988; 86%, Real et al. 2000). In Idaho, we administered carnidazole to 12 nestlings with trichomonosis. Without treatment, it is possible that trichomonosis would have caused the mortality of 38% (12/32) of Idaho eagle nestlings in 2015 as opposed to 0% with treatment.

Relatively low rates of *T. gallinae* infection in Golden Eagle breeding populations outside of Idaho may be related to the availability of historical prey populations (e.g., leporids and sciurids) or nesting habitat. At many of our sites outside of Idaho, Golden Eagles still primarily prey on mammals; Columbidae accounted for <5% of prey items in 37 individual prey studies used in a metapopulation study of Golden Eagle diets (Bedrosian et al. 2017), which is below the 10% critical threshold that we found predicts high likelihood of *T. gallinae* infection.

Although our results indicated a higher incidence of *T. gallinae* infection in Idaho than in other sites, the timing of sampling may have limited our detection of *T. gallinae* at sites outside of Idaho. Many samples from sites outside of Idaho were obtained from older nestlings (49–63 d old). Given that we documented *T. gallinae* infection developing when nestlings were 8–38 d old in Idaho, it is possible that *T. gallinae* could have already caused nestling mortality at sites outside of Idaho, thereby causing us to underestimate infection rates at those sites.

In addition to identifying *T. gallinae* through culture, we used molecular approaches to identify *T. gallinae*. Cultured swab samples and PCR results had a 53% agreement, which may be the result of several factors including death of trichomonads during transport or low numbers of trichomonads present in culture that precluded microscopic observation (Garber et al. 1987). It is possible that PCR-positive, but culture-negative, samples had low trichomonad density or had trichomonads that would not propagate in culture. In our study, the contents of each culture pouch were concentrated for DNA extraction and PCR, which allowed us the greatest chance to obtain a PCR-positive result from samples containing few live, or dead, trichomonads. The high proportion of false negatives in microscopy suggests the potential to underestimate positive samples, and therefore *T. gallinae* infection rates, within populations. Although cultures may have underestimated total *T. gallinae* presence, culturing swabs was a reliable indicator of the subsequent development of trichomonosis because we never detected lesions without first detecting *T. gallinae* in culture from an earlier visit.

Our documentation of *T. gypaetinii* represents, to our knowledge, a new geographic distribution for the protozoan, which has previously only been reported in Old World vultures (Martínez-Díaz et al. 2015). Given *T. gypaetinii* is morphologically similar to *T. gallinae*, only molecular analysis can distinguish the species, which underscores the importance of integrating classic and molecular analysis of *Trichomonas* spp. We observed the development of oral lesions similar to those caused by *T. gallinae* in 2/3 cases of *T. gypaetinii*; however, further laboratory studies are needed to determine the pathogenicity of *T. gypaetinii*.

Although we found oral pH decreased as nestlings aged, our results were similar to those of Urban and Mannan (2014) with mean nestling oral pH in older nestlings at 6.68; within the viable range for *T. gallinae* (Read 1957). Therefore, as nestlings approached fledging age, they were still susceptible to *T. gallinae* infection. It is unknown whether oral pH of Golden Eagles continues to decrease as young eagles age, but observations of trichomonosis in fledged Golden Eagles (Kochert 1972) suggests that the oral pH of young eagles may not be acidic enough to prevent infection.

Previous studies have found a positive association between columbids in raptor nestling diets and *T. gallinae* infection. Our study is the first to examine this association in Golden Eagles, a species that typically forages on mammals (Bedrosian et al. 2017). Further, we found that if eagle nestlings diets consisted of $\geq$10% Rock Pigeons, then nestlings had a high probability of *T. gallinae* infection. At our Idaho site, Golden Eagles consumed a higher proportion of Rock Pigeons compared to a historical period (1971–81), and the rate of trichomonosis (i.e., oral lesions) was higher in 2015 compared to the historical period. Historically, natural fluctuations in black-tailed jackrabbit abundance caused annual variation in nestling diet (Steenhof and Kochert 1988), periodically increasing risk of trichomonosis for nestlings. However, currently, landscape-level change in Idaho likely has resulted in dampened jackrabbit cycles and increased consumption of alternative prey such as Rock Pigeons (Heath and Kochert 2016). Although our study only measured *T. gallinae* and trichomonosis in 2015, rates of trichomonosis in Idaho Golden Eagle nestlings were similar in 2016 and 2017 (J.A.H. unpubl. data), suggesting that risk of trichomonosis may not fluctuate as much as in the historical period.

Although high rates of trichomonosis may negatively affect Golden Eagle populations, the availability of Rock Pigeons as prey could prove beneficial over time. In some European cities that support large Rock Pigeon populations, Northern Goshawk populations benefit from increased productivity because the abundance and availability of Rock Pigeons as prey outweighs the cost of reduced survival from high *T. gallinae* infection rates (Krone et al. 2005). Faced with the loss of historical prey populations, the abundance of Rock Pigeons as alternative prey may become beneficial for

Golden Eagle productivity in the future, despite the risk of *T. gallinae* infection.

Differences in infection rates between study sites, and between sampling periods in Idaho, may be explained by heterogeneity in the prevalence and virulence of *T. gallinae* within Rock Pigeon populations. Infection rates within Columbidae populations vary spatially and temporally (Rogers et al. 2016), and the transmission of *T. gallinae* in Rock Pigeon populations can occur through food and water sources (Villanúa et al. 2006). Therefore, infection rates can fluctuate based on annual temperature and precipitation (Rogers et al. 2016), and potential future variation in climatic conditions may affect the transmission of *T. gallinae* among columbids. Future studies of transmission rates and pathogenicity within Rock Pigeon populations, and how different strains manifest trichomonosis in raptor nestlings, will help us understand how infection rates in raptor populations may change over time and will be important in developing conservation strategies to manage protected species such as Golden Eagles.

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