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ECOLOGIC DRIVERS AND POPULATION IMPACTS OF AVIAN TRICHOMONOSIS MORTALITY EVENTS IN BAND-TAILED PIGEONS (*PATAGIOENAS FASCIATA*) IN CALIFORNIA, USA

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ABSTRACT: Avian trichomonosis, a disease typically caused by the protozoan parasite *Trichomonas gallinae*, is a well recognized cause of death in many avian species. In California, US, trichomonosis has caused periodic epidemics in Pacific Coast Band-tailed Pigeons (*Patagioenas fasciata monilis*). We summarize reported mortality events and investigate ecologic drivers and population impacts associated with epidemic mortality due to trichomonosis in Band-tailed Pigeons. Between 1945 and 2014, 59 mortality events involving Band-tailed Pigeons were reported in California with the number of reported events increasing over time. Estimated mortality for these events was variable, ranging between 10 and 10,000 pigeons. Events were most-frequently reported in Monterey (19%; 11/59) and San Luis Obispo (8%; 5/59) counties. Events often started in January (32%; 9/28) and February (50%; 14/28) and lasted 5–68 d. Impacts of mortality events on pigeon populations were indicated by Breeding Bird Survey and Christmas Bird Count abundance indices, which showed a decline in outbreak years compared to nonoutbreak years. Environmental conditions most associated with outbreak years included higher average temperatures between January and March, the period most associated with mortality events, and lower average precipitation in December just prior to mortality events. In Monterey County, events tended to occur in winters following higher acorn production of coast live oaks (*Quercus agrifolia*) in the fall. Weather and food abundance could be related to increased transmission or enhanced viability of *Trichomonas* spp. Although estimated mortality due to avian trichomonosis was highly variable across years, cumulative losses were substantial and likely to have a negative impact on population size.

Key words: Avian trichomonosis, Band-tailed Pigeon, California, disease, mortality, *Patagioenas fasciata*, population, upland game bird.

INTRODUCTION

Avian trichomonosis is typically caused by the protozoan *Trichomonas gallinae* and results in caseonectrotic (tissue death that appears crumbly or cheese-like) lesions in the upper digestive tract. Infection in wild birds ranges from subclinical to fatal for one to hundreds of birds (Forrester and Foster 2008). Trichomonosis has contributed to the decline of endangered Mauritian Pink Pigeons (*Columba mayeri*) and continues to hamper reintroduction efforts (Swinnerton et al. 2005; Bunbury et al. 2008). Recently, trichomonosis caused significant population declines in Greenfinch (*Carduelis chloris*) and Chaffinch (*Fringilla coelebs*) in Great Britain (Robinson et al. 2010). A large-scale trichomonosis mortality event occurred in Mourning Doves (*Zenaida macroura*) across the southeastern US between 1949 and 1951, when an estimated 25,000 doves died (Haugen 1952; Cole 1999; Shultz et al. 2005). In the western US, *T. gallinae* infections were first reported in free-ranging Rock Pigeons (*Columba livia*) of southern California in the late 1930s (Niemeyer 1939, *in* Stabler and Herman 1951) and in Mourning Doves in 1940 (Stabler and Herman 1951). In California, nearly annual trichomonosis events occurred in Mourning Dove populations between 1942 and 1949; these events typically occurred during spring and summer and involved less than a few hundred doves dying over several days (Stabler and Herman 1951). Events in Mourning Doves were primarily limited to individuals utilizing artificial feeding stations in urban areas in central and southern California.

While trichomonosis was identified early on as a disease of concern in Mourning Doves (Herman 1953), the same disease was not known to be a significant threat to the two subspecies of Band-tailed Pigeons (*Patagioenas fasciata*) occurring in the US (Keppie and Braun 2000). Both subspecies are partial migrants with the interior subspecies (*Patagioenas fasciata fasciata*) wintering in Mexico and breeding from Mexico north into Colorado and Utah and the Pacific Coast subspecies (*Patagioenas fasciata monilis*) wintering from central to southern California and breeding from California north into southeast Alaska. In a survey of 109 interior Band-tailed Pigeons in Colorado, 19% were infected with *T. gallinae* but infection was not associated with mortality (Stabler 1951). Among interior Band-tailed Pigeons in southern Arizona, prevalence of *T. gallinae* infection was 5%, but none of the 156 pigeons examined had oral lesions (Sileo and Fitzhugh 1969). A recent investigation involving Pacific Coast Band-tailed Pigeons in California found 5% of 322 birds were infected with *T. gallinae*, including three with oral lesions (Girard et al. 2014b). Pigeons of the interior subspecies developed oral and upper digestive tract lesions and died after being inoculated with parasites recovered from a dead Pacific Coast Band-tailed Pigeon (Stabler and Braun 1975). This suggests that Pacific Coast pigeons may harbor a strain of *Trichomonas* sp. that is more virulent than strains infecting pigeons of the interior US. Recently a novel strain, *Trichomonas stableri*, was isolated from Pacific Coast Band-tailed Pigeons during trichomonosis mortality events in California (Girard et al. 2014a). Stabler and Braun (1979) recommended investigation of *Trichomonas* spp. infection in Pacific Coast Band-tailed Pigeons to determine its significance as a pathogen.

The most publicly visible and often first-cited large-scale trichomonosis mortality event involving Band-tailed Pigeons occurred in 1988 in California, in which an estimated 16,000 pigeons died (Cole 1999). Since then, outbreaks of trichomonosis have continued to occur but, with some exceptions (Stromberg et al. 2008; Girard et al. 2014b), they have been only superficially investigated. Stromberg et al. (2008) estimated that an outbreak in the winter of 2006–07 killed over 43,000 pigeons in Monterey County. In-depth investigations into disease and mortality for Pacific Coast and interior Band-tailed Pigeons are critical because both populations are declining (Sanders 2013).

We reviewed the primary literature and mortality reports to compile all suspected and confirmed occurrences of large-scale mortality due to trichomonosis in Pacific Coast Band-tailed Pigeons. Ecologic factors during mortality events, including weather and food abundance, were explored as were the potential impacts of these events on the population. By evaluating the circumstances associated with known trichomonosis mortality events, we can begin to assess potential risk factors for epidemic transmission and mortality in this species.

MATERIALS AND METHODS

Mortality events

In addition to independent peer-reviewed publications dating back to the 1930s, trichomonosis occurrence in Band-tailed Pigeons was summarized recently by the US Geological Survey (USGS) National Wildlife Health Center (NWHC; Madison, Wisconsin, USA) (Cole 1999). The NWHC has been the repository for data on disease and mortality events in wildlife species in the US since 1975, with reports primarily submitted by state and federal resource agencies. Mortality events compiled by NWHC were obtained from the USGS (2016).

Documentation of disease events also occurred through mortality-event investigations by state agencies. In California, the California Department of Fish and Wildlife (CDFW) Wildlife Investigations Laboratory (WIL; Rancho Cordova, California, USA) has investigated disease and mortality in the state's wildlife since 1941. Documents retained by WIL were examined for descriptions of Band-tailed Pigeon mortality including accounts of sick or dead pigeons reported by department staff, the public, nonprofit organizations, or other government agencies. Investigations typically identified the wildlife species involved, number of individuals affected, location, and date. If carcasses were available, postmortem examination to identify trichomonosis was performed at WIL or the California Animal Health and Food Safety Laboratory (University of California, Davis, California, USA).

Reports of avian mortality also were available from the California Department of Public Health (CDPH; Richmond, California, USA) beginning in 2003 during surveillance for West Nile virus. Dead birds were reported by the public to CDPH via a toll-free telephone number or an online form available at www.westnile.ca.gov (accessed April 2016). These reports were provided to WIL staff for the investigation of avian mortality events.

Using the data sources described above, we compiled a comprehensive record of trichomonosis mortality events. A mortality event was defined as $\geq$5 reported or observed dead or dying pigeons within a <300 km^2 area over a period of <90 d. As expected, the level of detail among mortality reports was highly variable. Events were included in the summary if they met the following criteria: 1) bird species identified as Band-tailed Pigeon; 2) location described (county); 3) cause of mortality identified as trichomonosis by the presence of caseous oral lesions during postmortem examination; or (for older records) clinical signs indicative of trichomonosis (e.g., emaciation, labored breathing, excessive salivation); or one or more birds positive for *Trichomonas* sp. by culture, PCR, immunohistochemistry, or wet mount from an oropharyngeal swab sample.

Mortality events were evaluated for duplications among the various data sources, and events occurring within <300 km^2 during exactly the same time frame were combined and counted as one event. Events that reportedly covered larger geographic areas were split to include each county in which mortality was reported. The accuracy of each event location was qualified as exact, city-based, or county-based. Exact locations were derived from complete street address or GPS coordinates. City-based locations were determined from a landmark, street name, or city name. County-based locations were derived from favorable habitat or a previously documented event location within the county.

Bird abundance

Breeding Bird Survey (BBS) data were obtained from the USGS Patuxent Wildlife Research Center (Sauer et al. 2014). Briefly, BBS population index data were calculated from point counts conducted along designated survey routes each year between late May and early July (Sauer and Link 2011). Christmas Bird Count (CBC) data were obtained from the National Audubon Society (2014). The CBC took place annually between mid-December and mid-January. A point count was conducted within designated count circles, and the "mean number of birds counted per party hour," or index, was calculated for each bird species recorded (Butcher 1990). Because the mortality events may affect the entire population, a regional (California, Oregon, Washington, and British Columbia) average annual index for Pacific Coast Band-tailed Pigeons was calculated between 1968 and 2012 for BBS data and between 1960 and 2012 for CBC data. The index values for BBS and CBC were matched with mortality event data for the prior winter. Years were identified as "outbreak" if one or more trichomonosis mortality events were reported and as "nonoutbreak" if events were not reported.

Weather variables

Because mortality events rarely occurred in the same exact geographic location from year to year, statistical analysis of weather variables for consecutive years at each location was not possible. Due to California's size and highly varying climate, we elected not to use a single average of each weather variable for the entire state. Alternatively, we directly compared weather variables at a given location during an outbreak year vs. the preceding or the following nonoutbreak year for 30 locations (see Supplementary Material Table S1) to obtain a general trend for weather conditions during outbreak years. The number of locations in which the select weather variable was higher or lower between the event year and nonevent year were calculated to test for an association between weather conditions and epidemic avian trichomonosis. Weather variables included monthly average temperature (C) for November–March for the outbreak year and the comparison nonoutbreak year. In addition, temperature was averaged over the months of November–January and January–March because outbreaks were most often reported before or during these periods, respectively. Average precipitation (mm) was calculated for each month between November and March and over November–January. These weather variables were also collected for Monterey County for inclusion in the acorn production analysis for that county. Data for weather variables were obtained from the PRISM Climate Group (Northwest Alliance for Computational Science & Engineering 2016).

Acorn production

Acorns are the primary food item of Band-tailed Pigeons during the winter (Keppie and Braun 2000), the period when trichomonosis mortality events are most-often reported. To determine if there was an association between

TABLE 1. Number of counties with reported avian trichomonosis mortality events involving Band-tailed Pigeons (*Patagioenas fasciata monilis*) in California, USA for the time period shown.

Time period	Number of events
1945–49	2
1950–54	1
1955–59	0
1960–64	0
1965–69	1
1970–74	3
1975–79	4
1980–84	1
1985–89	10
1990–94	1
1995–99	5
2000–04	4
2005–09	12
2010–14	15

food availability and mortality event occurrence, we compared acorn production for years in which mortality events were reported to years without mortality events. Acorn production in Monterey County, California was selected for analysis because acorn survey data were available for the longest period coinciding with the highest number of reported mortality events; similar acorn production data are not available for other event locations. Acorn production was determined by visual surveys of oak trees on the Hastings Natural History Reservation. At Hastings, acorn surveys of *Quercus agrifolia* (n=62), *Quercus chrysolepis* (n=21), *Quercus douglasii* (n=56), *Quercus kelloggii* (n=19), and *Quercus lobata* (n=86) were conducted annually between 1987 and 2013. Koenig et al. (1994) provide a detailed account of acorn survey methods. In short, acorn counts were conducted annually in September on the same set of trees at each location. Two observers counted acorns on different areas of the canopy for 15 s. Counts were added to yield the number of acorns per 30 s (N30). The N30 values were averaged to generate the mean estimate of acorn crop for each oak species in a given year. Mean N30 values were matched with mortality event data; the latter lagged by 1 yr.

Statistical analysis

We analyzed differences in reported month and location of mortality events using the chi-square (χ^2) test of independence. We compared BBS and CBC average annual indices between event and nonevent years using Mann-Whitney U-tests. We used binary logistic regression to determine the relative effect of different variables on the probability of a mortality event occurring in Monterey County in a given year; mean temperature, precipitation, and acorn production of each oak species were entered as factors. Statistical analyses were performed using NCSS (Hintze 2007). Values reported are mean±SE and $P \leq 0.05$ was considered statistically significant. Median, first quartile (Q1), and third quartile (Q3) are presented where appropriate. Maps were prepared using ArcMap (ESRI, Inc. 2010).

RESULTS

Mortality events

Between 1945 and 2014, 59 mortality events were reported in Band-tailed Pigeons in 27 counties (see Supplementary Material Table S2). At least one trichomonosis mortality event was reported in 19 of the 70 (27%) years evaluated, with the number of counties with reported events increasing over time (Table 1). Approximately 47% (28/59) of the mortality events had an estimated event start date and, of these, 71% (20/28) had an estimated event end date. Most (54/59) events had a “date reported,” so there was an approximate time frame for when the event occurred. Mortality event start dates were reported in December (11%, 3/28), January (32%, 9/28), February (50%, 14/28), March (4%, 1/28), and April (4%, 1/28) (χ^2=29.29, df=4, P<0.001). Event end dates were reported in January (15%, 3/20), February (30%, 6/20), March (50%, 10/20), and April (5%, 1/20) (χ^2=12.27, df=3, P=0.007). The median duration for mortality events with known start and end dates was 31 d (n=20; Q1: 12, Q3: 45).

The exact mortality event location was identified for 27% (16/59) of the events, 46% (27/59) had a city-based designation, and 27% (16/59) had a county-based designation (Fig. 1). Events were most-frequently reported in Monterey (19%, 11/59), San Luis Obispo (8%, 5/59), and El Dorado (7%, 4/59) counties (χ^2=3.82, df=26, P=0.001; Fig. 2). The remaining events were reported from counties shown in Figure 2. Events were more-

FIGURE 1. Location accuracy for avian trichomonosis mortality events involving Band-tailed Pigeons (*Patagioenas fasciata monilis*) reported in California, USA 1945–2014. Exact location was determined based upon street address or geographic coordinates; city-based location was determined from an identifiable landmark, street name, or city name; and county-based location was identified at the county level.

frequently reported in counties within the Coastal Mountain Range (61%, 36/59) than within the Sierra Nevada Mountain Range (39%, 23/59) (χ^2=5.73, df=1, P=0.02; Fig. 2).

Estimated mortality for Band-tailed Pigeons was reported for only 51% (30/59) of the events (see Supplementary Material Table S2). The median estimated mortality was 200 pigeons (n=30; Q1: 35, Q3: 375). However, estimates of mortality are generally underestimated given the difficulty in obtaining accurate mortality counts for lengthy outbreaks in remote locations and poor carcass detection due to decomposition and scavenging.

Mortality events that took place between December 2011 and March 2012 occurred during active surveillance for trichomonosis in Band-tailed Pigeons (Girard et al. 2014b). These events were reported at eight locations in eight counties with site visits conducted at six locations. The number of pigeons found sick or dead was recorded during each site visit and via follow-up monitoring by local

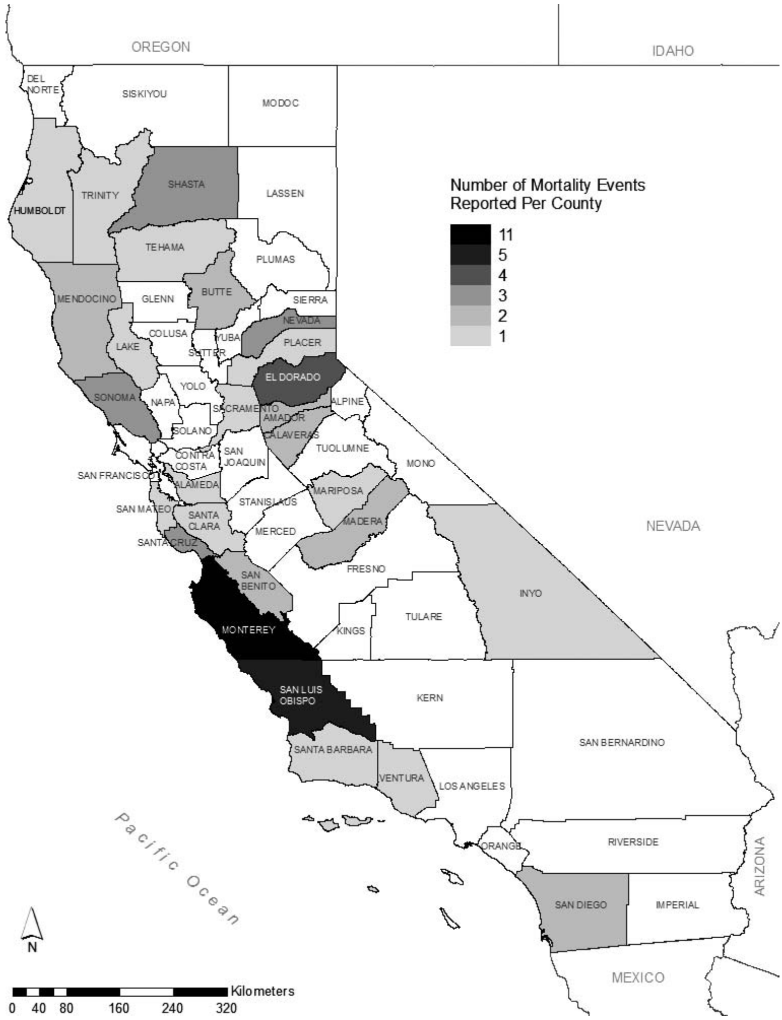

FIGURE 2. Number of avian trichomonosis mortality events involving Band-tailed Pigeons (*Patagioenas fasciata monilis*) reported per county in California, USA 1945–2014.

personnel for the duration of the event. Total estimated mortality calculated for these events was 9,750 pigeons (n=8, median 40, Q1: 30, Q3: 1,500).

Bird abundance

The BBS average annual index for Pacific Coast Band-tailed Pigeons was significantly lower during outbreak years (6.08±0.43, n=15) compared to nonoutbreak years (7.47±0.41, n=30; Mann-Whitney U-test: Z=–2.41, P=0.02). The CBC average annual index for Band-tailed Pigeons was significantly lower during outbreak years (0.44±3.97E-02, n=16) vs. nonoutbreak years (0.72±8.08E-02, n=37; Mann-Whitney U-test: Z=–2.20, P=0.03).

Weather variables

The 30 locations used for comparison of weather variables are indicated in Supplementary Material Table S1. Average temperatures for January (P=0.02) and the period between January and March (P=0.005) were higher during outbreak years vs. nonoutbreak years while average temperature for November was lower in outbreak years (Table 2). Average precipitation for December

TABLE 2. Comparisons of weather variables at 30 locations in California, USA in which a trichomonosis mortality event was reported in Band-tailed Pigeons (*Patagioenas fasciata monilis*). Count (%) of locations in which the temperature or precipitation values were higher and lower during the outbreak year compared with values during the same time period in the comparison nonoutbreak year.

Weather variable	During the outbreak year, the select weather variable was: Higher	Lower	*P*
Average temperature (°C)			
November	8 (27)	22 (73)	0.016*
December	17 (57)	13 (43)	0.585
January	22 (73)	8 (27)	0.016*
February	20 (67)	10 (33)	0.099
March	14 (47)	16 (53)	0.856
November–January	19 (63)	11 (37)	0.200
January–March	23 (77)	7 (23)	0.005*
Average precipitation (mm)			
November	13 (43)	17 (57)	0.585
December	7 (23)	23 (77)	0.005*
January	17 (57)	13 (43)	0.585
February	21 (70)	9 (30)	0.043*
March	21 (70)	9 (30)	0.043*
November–January	3 (10)	27 (90)	0.001*

* $P<0.05$; one proportion test.

($P=0.005$) and November–January ($P<0.001$) was lower in outbreak than in nonoutbreak years while average precipitation was higher in February and March in outbreak years (Table 2). See Table 2 for remaining weather variable comparisons.

Acorn production

Mean acorn production in Monterey County for *Q. agrifolia* was significantly higher in the year preceding an outbreak year (outbreak 25.86±5.82, $n=7$; nonoutbreak 10.98±2.70, $n=20$; logistic regression: Wald $Z=-2.14$, $P=0.02$). Correlations with acorn production for the remaining four oak species and weather variables for Monterey County were not significant ($P>0.05$).

DISCUSSION

We identified 59 confirmed and suspected avian trichomonosis mortality events in Pacific Coast Band-tailed Pigeons in California between 1945 and 2014. Band-tailed Pigeon populations have been declining for at least the past 40 yr, with BBS annual counts declining 2.1% per year between 1968 and 2012 (Sauer et al. 2014). The median count of Band-tailed Pigeons has declined 4.7% per year between 2004 and 2012 according to the Mineral Site Survey, which is conducted annually in July and is specifically designed to monitor population trends of Pacific Coast Band-tailed Pigeons (Sanders 2013). This decline is also reflected in the substantial reduction of hunter bag limits and seasons for Band-tailed Pigeons over the last 20 yr (Sanders 2013). Our analysis, which detected temporal correlations between trichomonosis outbreaks in Band-tailed Pigeons and two independent measures of annual bird abundance, suggests that trichomonosis mortality events are contributing to the decline of this species.

Although mortality of Band-tailed Pigeons in California due to trichomonosis occurs year-round (Girard et al. 2014b), large-scale mortality events have only been documented December–April. It is still unknown whether migratory or resident pigeons are more likely to be involved in large-scale mortality. Pigeons that breed in the northern part of the range (British Columbia, Washington, Oregon, and northern California) migrate south to winter in central and southern California (Keppie and Braun 2000). During this time, pigeons form large flocks that persist through spring migration, the timing of which is tied to food availability and weather (Neff 1947; Keppie and Braun 2000). Resident birds that persistently shed parasites may act as a disease reservoir for migratory birds, a possibility which is supported by the majority of reported events occurring in the more southerly to central part of the range where migratory and resident birds co-occur during the winter.

We observed temporal and spatial patterns in the 2011–12 mortality events which suggest Band-tailed Pigeons wintering in southern and central California are most vulnerable to trichomonosis-related mortality. Events affecting larger numbers of individuals were first observed in southern to central California while subsequent reports of mortality affecting fewer individuals occurred in central to northern California. Mortality would decrease as migration progresses if large numbers of pigeons died before continuing migration, leaving fewer susceptible individuals along the more northerly aspects of the migration route.

Of the 29 reported events with estimated mortality, 17 had estimated mortality of over 100 birds. More important is the timing of these events, which disproportionally affects adult pigeons, the demographic most likely to influence population productivity. Jarvis and Passmore (1992) found that after-second-year Band-tailed Pigeons breeding in Oregon produced 94% of the juveniles compared to second-year birds, indicating that adult pigeons are critical to population stability. In addition, they identified distinct periods of population increase and decrease between 1950 and 1988 based on Oregon Mineral Site Survey data. Aligning these findings with historical trichomonosis mortality event occurrence in California, we find that during the two periods of increase from 1950 through the mid-1960s, there was one event in 1953 and from the mid-1970s through the early 1980s there was one event in 1982. By contrast, during the two periods of population decrease from the mid-1960s through the mid-1970s, there were 8 events in 3 yr and from the mid-1980s to 1988 there were 10 events in 2 yr. This supports the speculation of Jarvis and Passmore (1992) that excessive mortality was the cause for the declines. The increasing frequency of reported mortality events in California, with 36 events reported in the last 20 yr, demonstrates that trichomonosis is a significant emerging infectious disease of Pacific Coast Band-tailed Pigeons, possibly contributing to a decline in breeding adults in the northern part of their range. High adult mortality and increased frequency of events, when coupled with low recruitment (1.26 juveniles per female; Keppie and Braun 2000), suggests annual recruitment may not keep pace with adult mortality, leading to population decline.

Our analysis of weather variables indicates that temperature and precipitation may be correlated with outbreak occurrence. Generally, mortality events occurred during winter with higher average temperatures between January and March, the period most associated with mortality events and lower average precipitation in December, just prior to mortality events. Temperature was lower in November, before mortality events occurred, and precipitation was higher in February and March toward the end of mortality events. Similarly, Bunbury et al. (2007) found higher prevalence of *T. gallinae* infection for Madagascar Turtle Doves (*Streptopelia picturata*) sampled at warmer and drier sites and months in Mauritius. In California, it is possible that parasite viability is enhanced during winter months in years with moderately warmer conditions (Kocan 1969). Bunbury et al. (2007) also found higher prevalence of *T. gallinae* infection for doves sampled at coastal locations compared to inland locations. Similar conditions may exist in California, where coastal temperatures are generally warmer and average less precipitation than in the Sierra Nevada, explaining why more outbreaks were reported along the coast. Likewise, resident Band-tailed Pigeons, and possibly other sympatric species, in warmer and drier regions of southern California may act as a reservoir for *Trichomonas* spp., infecting migratory Band-tailed Pigeons during winter.

Previous studies (Stabler 1954; Kocan 1969) have identified water as an important vehicle for *T. gallinae* transmission. Gerhold et al. (2013) found that *T. gallinae* persisted longer in water containing organic matter and suggested that water sources containing rain or well water may present a greater risk of parasite transmission. Recent observations indicate that Band-tailed Pigeon mortality tended to occur near available water sources. As a result of a relatively dry December in 2011, water flow in the streams where the pigeons drank was reduced. For at least seven of eight locations where mortality events were reported in 2011–12, pigeon mortality appeared to be concentrated around pools of stagnant or slow-moving water. Similarly, during the 2013–14 mortality event, sick pigeons were seen drinking from local streams, retention ponds, and cattle troughs alongside apparently healthy pigeons. Low precipitation early in winter results in slower-moving streams and fewer streams with water available, thereby concentrating pigeons around fewer natural water sources and possibly increasing use of artificial sources. This may accelerate parasite transmission between congregating individuals and aid in detection of mortality events. More research is needed to identify potential host species and routes of transmission that facilitate infection in Band-tailed Pigeons, particularly in winter.

In this study, acorn abundance of coast live oaks in Monterey County during the fall correlated with mortality event occurrence, with events more likely to occur in winters following higher acorn production. During winter, Band-tailed Pigeons rely most heavily on acorns for food, and diet analyses have shown that acorns of *Q. agrifolia* were frequently represented (Neff 1947; Smith 1968). *Quercus agrifolia* is unique among oak species in that it may retain acorns into February or March while most other oaks have lost their acorns by December (Koenig et al. 2014). Site-specific fluctuations in acorn production and retention between years would result in variable use by pigeons, explaining why mortality events are infrequently documented in some locations. Recent observations made during mortality event site visits support the finding of high acorn abundance at mortality event locations and, consequently, high use by pigeons. Further, acorn retention by *Q. agrifolia* was more likely to occur in winters with lower precipitation (Koenig et al. 2014), suggesting high acorn abundance and low precipitation may work in tandem to further concentrate pigeon populations, thus increasing the likelihood of propagated disease transmission cycles.

We have shown that avian trichomonosis mortality events had a negative impact on population abundance of Pacific Coast Band-tailed Pigeons. The increasing frequency of these events, with events occurring in six of the last 10 yr, is additive to losses due to predation, hunting, and other trauma (e.g., window collisions, poaching), with the potential cumulative impacts threatening persistence of this species if unabated. To better manage Band-tailed Pigeon populations, we need to understand how habitat use, diet, weather, parasite characteristics (e.g., genetics, viability, and virulence), cross-species disease transmission, and individual susceptibility to infection influence the probability of large-scale mortality events.

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SUPPLEMENTARY MATERIAL

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LITERATURE CITED

Bunbury N, Jones CG, Greenwood AG, Bell DJ. 2007. *Trichomonas gallinae* in Mauritian Columbids: Implications for an endangered endemic. *J Wildl Dis* 43: 399–407.

Bunbury N, Jones CG, Greenwood AG, Bell DJ. 2008. Epidemiology and conservation implications of *Trichomonas gallinae* infection in the endangered Mauritian Pink Pigeon. *Biol Conserv* 141:153–161.

Butcher GS. 1990. Audubon Christmas bird counts. In: *Survey designs and statistical methods for the estimation of avian population trends*, Sauer JR, Droege S, editors. Biological Report 90(1), US Fish and Wildlife Service, Laurel, Maryland, pp. 5–13. http://digitalmedia.fws.gov/cdm/ref/collection/document/id/1775. Accessed March 2014.

Cole RA. 1999. Trichomoniasis. In: *Field guide to wildlife disease: General field procedures and diseases of birds*, Friend M, Franson JC, editors. US Fish and Wildlife Service Information and Technology Report 1999–2001, Biological Resources Division, US Geological Survey, Washington, DC, pp. 201–206. http://www.nwhc.usgs.gov/publications/field_manual/chapter_25.pdf. Accessed January 2014.

ESRI, Inc. 2010. ArcMap. Version 10.0. ESRI, Inc., Redlands, California. http://desktop.arcgis.com/en/arcmap/. Accessed April 2016.

Forrester DJ, Foster GW. 2008. Trichomonosis. In: *Parasitic diseases of wild birds*, Atkinson CT, Thomas NJ, Hunter DB, editors. Wiley-Blackwell, Ames, Iowa, pp. 120–153.

Gerhold RW, Maestas LP, Harnage PM. 2013. Persistence of two *Trichomonas gallinae* isolates in chlorinated and distilled water with or without organic material. *Avian Dis* 57:681–683.

Girard YA, Rogers KH, Gerhold R, Land KM, Lenaghan SC, Woods LW, Haberkern N, Hopper M, Cann JD, Johnson CK. 2014a. *Trichomonas stableri* n. sp., an agent of trichomonosis in Pacific Coast Band-tailed Pigeons (*Patagioenas fasciata monilis*). *Int J Parasitol: Parasites Wildl* 3:32–40.

Girard YA, Rogers KH, Woods LW, Chouicha N, Miller WA, Johnson CK. 2014b. Dual-pathogen etiology of avian trichomonosis in a declining Band-tailed Pigeon population. *Infect Genet Evol* 24:146–156.

Haugen AO. 1952. Trichomoniasis in Alabama mourning doves. *J Wildl Manage* 16:164–169.

Herman CM. 1953. Recognition of trichomoniasis in doves. *Bird-Banding* 24:11–12.

Hintze J. 2007. NCSS. Statistical software. Version 07.1.21. NCSS, LLC., Kaysville, Utah. www.ncss.com. Accessed April 2016.

Jarvis RL, Passmore MF. 1992. Ecology of Band-tailed Pigeons in Oregon. Biological Report 6. US Department of the Interior, Fish and Wildlife Service, Washington, DC, 38 pp.

Keppie DM, Braun CE. 2000. Band-tailed Pigeon (*Columba fasciata*). In: *The birds of North America*, No. 530, Poole A, Gill F, editors. The Birds of North America, Inc., Philadelphia, Pennsylvania, 27 pp.

Kocan RM. 1969. Various grains and liquid as potential vehicles of transmission for *Trichomonas gallinae*. *J Wildl Dis* 5:148–149.

Koenig WD, Mumme RL, Carmen WJ, Stanback MT. 1994. Acorn production by oaks in central coastal California: Variation within and among years. *Ecology* 75:99–109.

Koenig WD, Walters EL, Pearse IS, Carmen WJ, Knops JMH. 2014. Serotiny in California oaks. *Madroño* 61: 151–158.

Northwest Alliance for Computational Science & Engineering. 2016. *PRISM climate data*. http://www.prism.oregonstate.edu. Accessed April 2016.

National Audubon Society. 2014. The Christmas bird count historical results. http://www.christmasbirdcount.org. Accessed March 2014.

Neff JA. 1947. Habits, food, and economic status of the Band-tailed Pigeon. *North American fauna* 58. US Fish and Wildlife Service, Washington, DC, 76 pp.

Robinson RA, Lawson B, Toms MP, Peck KM, Kirkwood JK, Chantrey J, Clatworthy IR, Evans AD, Hughes LA, Hutchinson OC, et al. 2010. Emerging infectious disease leads to rapid population declines of common British birds. *PLoS One* 5:e12215.

Sanders TA. 2013. *Band-tailed Pigeon population status, 2013*. US Fish and Wildlife Service, Division of Migratory Bird Management, Washington, DC, 20 pp. http://www.fws.gov/migratorybirds/NewsPublicationsReports.html. Accessed January 2014.

Sauer JR, Hines JE, Fallon JE, Pardieck KL, Ziolkowski DJ Jr, Link WA. 2014. In: *The North American breeding bird survey, results and analysis 1966–2011, version 09.19.2014*. US Geological Survey, Patuxent Wildlife Research Center, Laurel, Maryland. http://www.mbr-pwrc.usgs.gov/bbs/bbs.html. Accessed April 2016.

Sauer JR, Link WA. 2011. Analysis of the North American breeding bird survey using hierarchical models. *Auk* 128:87–98.

Shultz JH, Bermudez AJ, Millspaugh JJ. 2005. Monitoring presence and annual variation of trichomoniasis in Mourning Doves. *Avian Dis* 49:387–389.

Sileo L Jr, Fitzhugh EL. 1969. Incidence of trichomoniasis in the Band-tailed Pigeons of southern Arizona. *J Wildl Dis* 5:146.

Smith WA. 1968. The Band-tailed Pigeon in California. *Calif Fish Game* 54:4–16.

Stabler RM. 1951. A survey of Colorado Band-tailed Pigeons, Mourning Doves, and wild common pigeons for *Trichomonas gallinae*. *J Parasitol* 37:471–472.

Stabler RM. 1954. *Trichomonas gallinae*: A review. *Exp Parasit* 3:368–402.

Stabler RM, Braun CE. 1975. Effect of virulent *Trichomonas gallinae* on the Band-tailed Pigeon. *J Wildl Dis* 11:482–483.

Stabler RM, Braun CE. 1979. Effects of a California-derived strain of *Trichomonas gallinae* on Colorado Band-tailed Pigeons. *Calif Fish Game* 65:56–58.

Stabler RM, Herman CM. 1951. Upper digestive tract trichomoniasis in Mourning Doves and other birds. In: *Transactions of the Sixteenth North American Wildlife Conference*, Milwaukee, Wisconsin, 5–7 March 1951, Wildlife Management Institute, Washington, DC, pp. 145–163.

Stromberg MR, Koenig WD, Walters EL, Schweisinger J. 2008. Estimate of *Trichomonas gallinae*-induced mortality in Band-tailed Pigeons, Upper Carmel Valley, California, Winter 2006–2007. *Wilson J Ornithol* 120:603–606.

Swinnerton KJ, Greenwood AG, Chapman RE, Jones CG. 2005. The incidence of the parasite disease trichomoniasis and its treatment in reintroduced and wild Pink Pigeons *Columba mayeri*. *Ibis* 147:772–782.

US Geological Survey (USGS). 2016. *Quarterly mortality reports*. http://www.nwhc.usgs.gov/publications/quarterly_reports/index.jsp. Accessed April 2016.

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