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AVIAN HEMOSPORIDIAN PARASITES FROM NORTHERN CALIFORNIA OAK WOODLAND AND CHAPARRAL HABITATS

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ABSTRACT: During spring–summer 2003–2004, the avian community was surveyed for hemosporidian parasites in an oak (*Quercus* spp.) and madrone (*Arbutus* spp.) woodland bordering grassland and chaparral habitats at a site in northern California, a geographic location and in habitat types not previously sampled for these parasites. Of 324 birds from 46 species (21 families) sampled (including four species not previously examined for hemosporidians), 126 (39%) were infected with parasites identified as species of one or more of the genera *Plasmodium* (3% of birds sampled), *Haemoproteus* (30%), and *Leucocytozoon* (11%). Species of parasite were identified by morphology in stained blood smears and were consistent with one species of *Plasmodium*, 11 species of *Haemoproteus*, and four species of *Leucocytozoon*. We document the presence of one of the parasite genera in seven new host species and discovered 12 new parasite species–host species associations. Hatching-year birds were found infected with parasites of all three genera. Prevalence of parasites for each genus differed significantly for the entire sample, and prevalence of parasites for the most common genus, *Haemoproteus*, differed significantly among bird families. Among families with substantial sample sizes, the Vireonidae (63%) and Emberizidae (70%) were most often infected with *Haemoproteus* spp. No evidence for parasite between-genus interaction, either positive or negative, was found. Overall prevalence of hemosporidians at the northern California sites and predominance of *Haemoproteus* spp. was similar to that reported in most other surveys for the USA, Canada, and the Caribbean islands.

Key words: Avian malaria, California, *Haemoproteus*, Hemosporidia, *Leucocytozoon*, *Plasmodium*.

INTRODUCTION

The avian hemosporidian parasites (phylum Apicomplexa) are taxonomically diverse, cosmopolitan in distribution, and have been reported infecting hosts from most bird families (Valkiunas, 2005). More than 200 described species are classified into three genera, *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*. Levine (1988) places the three genera into a single family, the Plasmodiidae, whereas Valkiunas (2005) separates *Leucocytozoon* into its own family, the Leucocytozoidae. The broad landscape ecology and transmission dynamics of parasites of the three genera are likely to differ because parasites placed into different genera exploit different taxa of blood-feeding vectors with different habitats and biting behavior. *Haemoproteus* spp. are transmitted by biting midges (Ceratopogonidae) and hippoboscid flies (Hippoboscidae), *Plasmodium* spp. by mosquitoes (Culicidae), and *Leucocytozoon* spp. by blackflies (Simuliidae) (Valkiunas, 2005).

Surveys of local bird assemblages completed in many regions of the world suggest that the prevalence of parasites placed into *Plasmodium*, *Haemoproteus*, and *Leucocytozoon* differs geographically. For example, *Leucocytozoon* spp. appear common in birds of temperate regions, even including high latitudes in the subarctic, but are rare or absent from neotropic locations (Greiner et al., 1975; White et al., 1978; Valkiunas, 1996, 2005). Such patterns may be driven by habitat quality affecting host and vector density and the systematic composition of the bird communities. The latter possibility is particularly intriguing because the prevalence of hemosporidians appears to vary among bird families perhaps because of

differential susceptibility and other host-parasite interactions (Greiner et al., 1975). Although parasites in the three genera have the same basic life cycle, differences in vertebrate host tissues infected and intensity of blood stages may lead to different levels of virulence. *Plasmodium* spp. and *Leucocytozoon* spp. are viewed as the more virulent parasites, although *Haemoproteus* spp. have also been shown to be detrimental to their avian hosts (Atkinson and van Riper, 1991; Valkiunas, 1993; Valkiunas 2006). Thus, variation in prevalence and virulence of parasites placed in the three genera must play a role in the parasite-host biology of avian hemosporidians, including their overall importance for the ecology of their bird hosts.

Local surveys for malaria parasites and other hemosporidians in North American bird communities have been unevenly distributed both geographically and taxonomically, with most studies grouped in the eastern USA and southern Canada, with a focus on perching birds (Passeriformes). Only a few surveys have been reported for California, USA, birds: the Sacramento region in the Central Valley (Herman et al., 1954; Clark and Swinehart, 1966), an island and mainland northern coastal scrub habitat (Super and van Riper, 1995), and the Los Angeles region and southward (Wood and Wood, 1937; Herms et al., 1939). Here, we report the first survey from northern California from an oak/madrone woodland bordering open grass and an oak woodland bordering chaparral, habitats characteristic of the valleys of the coastal ranges. Our goals in this study were 1) to determine the prevalence of hemosporidian parasites, identified to genus and species, in a complex avian community that has not been surveyed before, with an emphasis on the relative prevalence of parasites of the three genera *Plasmodium, Haemoproteus*, and *Leucocytozoon*; 2) to document the host range of the parasites, including bird species that have not previously been shown to be hosts for hemosporidians; 3) to determine whether hatching-year birds are infected, an indication of transmission at the study sites; 4) to determine whether parasites for the three genera differ in prevalence by bird family; 5) to examine the data for suggestions of interactions between parasites of the three genera; and 6) to compare the prevalence results with those from other surveys of avian hemosporidian parasites.

METHODS

The study location was the Hopland Research and Extension Center (HREC), a 2,169-ha tract located near the town of Hopland in southern Mendocino County, California, USA (39°00′22″N, 123°05′13″W). The climate at Hopland is Mediterranean, with hot, dry summers and cool, wet winters. Annual rainfall averages 937 mm, and July to August maximum temperature averages 33 C (HREC records from 1953 to 2000). Twelve collecting sites were selected over an elevational gradient from 320 to 810 m. Lower-elevation sites were oak/madrone woodland bordering open grass habitat, dominated by *Quercus* spp. and Pacific madrone (*Arbutus menziesii*). Habitats in higher sites were oak woodland bordering chaparral. These are typical habitats of coastal valleys and ridges. Further information on these sites is presented in Eisen et al. (2004, 2005). Birds were captured by mist-nets, without any use of call playback to prevent luring in birds from other habitats. Each captured bird was identified to species and age based on criteria in Pyle (1997), and a blood sample taken by brachial venipuncture. Thin smears were made on microscope slides, fixed in the field with absolute methanol, and later stained with Giemsa stain (pH 7.0). Smears were examined first at 100× for 3–5 min (approximately 2×10^6 blood cells examined) for detection of *Leucocytozoon* spp. infections with low parasitemia. *Leucocytozoon* parasites are obvious un-

der 100× magnification, as are most gametocytes of *Haemoproteus* spp. and *Plasmodium* spp. Each slide was then examined under 1,000× for an additional 5–8 min (approximately 3×10^4 blood cells). Smears from infected birds were then examined at 1,000× for the entirety of the slide (upwards of 1 hr) to examine many parasite cells for identification to genus and species. All slides are on deposit at the University of Vermont Thompson Zoology collections.

Identification of parasites was based on Valkiunas (2005) and numerous original species descriptions. We present identifications of parasites to genus with confidence because *Leucocytozoon* is distinct in morphology from the other genera, and with experience, the difference between gametocytes of *Plasmodium* and *Haemoproteus* is also clear. However, identification to species has long been a challenge for those working with the avian hemosporidians and requires inspection of many parasite cells in a blood smear because morphologic characteristics overlap for many similar pairs of species (Valkiunas, 2005). Unfortunately, very low-intensity infections are common for all three parasite genera, with rather few parasite cells to examine on many smears. In the current study, we identified parasites to species only when ample parasitemia and morphology allowed us to do so with confidence. Nonetheless, we report identifications only as "consistent with the morphology" of described species because the union of morphologic and molecular systematics for these parasites is only in its infancy (Krizanauskiene et al., 2006; Martinsen et al., 2006). Collection of birds and blood samples followed protocols of state, federal, and University of California Animal Care and Use permits.

RESULTS

Blood smears from 324 birds of 46 species and 21 avian families were examined, including four species that have not previously been sampled for avian hemosporidians. A total of 126 birds were infected with parasites of one or more of the genera (39% of birds), 10 with *Plasmodium* spp., 96 with *Haemoproteus* spp., and 36 with *Leucocytozoon* spp. (Table 1). Overall prevalence of parasites within the three genera differed significantly. *Haemoproteus* spp. were the most common parasites (30% of all birds examined, 76% of birds with an infection [95% confidence interval {CI}=0.68−0.83]), *Leucocytozoon* spp. were also common (11% and 29% [CI=0.21–0.37]), and *Plasmodium* spp. rare (3% and 9% [CI=0.03–0.14]). Table 1 presents the bird species in the sample by family, infection status by genus and species, and documentation of infection by parasites from the three genera reported in previous studies (Bennett et al., 1982; Bishop and Bennett, 1992; Herman 1944; Super and van Riper, 1995). Three host species are first reported as infected with parasites of the genus *Plasmodium*, two host species with parasites of the genus *Haemoproteus*, and two host species with parasites of the genus *Leucocytozoon*. One species of *Plasmodium* (and two infections identified only to subgenus), 11 species of *Haemoproteus*, and four species of *Leucocytozoon* were identified; parasites in many other infections could be identified only to genus because parasitemia was too low for examination of many parasite cells (Table 1). One species of *Haemoproteus* found in a Bushtit (*Psaltriparus minimus*) did not resemble any described species in the genus and, thus, probably represents a new taxon. Ten of the identified species were found only in a single bird species, and the others were found in two to 10 bird species. *Haemoproteus fringillae* appeared to have the broadest host range, being identified in 10 bird species of four families. Twelve new host species–parasite species associations were documented. Four species of flycatcher (Tyrannidae) were sampled; only one of 17 birds was infected. Four species of woodpeckers (Picidae) did not harbor any hemospori-

TABLE 1. Presence of hemosporidian parasites of three genera, *Haemoproteus* (*H.*), *Leucocytozoon* (*L.*), and *Plasmodium* (*P.*) in birds sampled at several sites at the Hopland Research and Extension Center in Mendocino County, California, USA. Sample size of each bird species is given (*n*), with number of birds scored as infected with a parasite by genus. When sufficient parasite cells were present on a blood smear, identifications to species are given (in two cases, an infection is identified to the *Plasmodium* subgenus *Haemamoeba*). An undescribed species of *Haemoproteus* was sampled in the Bushtit and is indicated. Previously reported results are also summarized, listing parasites of which genus, if any, that have been found infecting each bird (giving genus code, based on numerous reports, including Bennett et al., [1982]; Bishop and Bennett [1992]; Herman [1944]; and Super and van Riper [1995]). New host-parasite species associations are indicated in bold.

Birds family, common name, taxonomy	*n*	*H.*	*L.*	*P.*	Parasite species	Previous
Turdidae						
American Robin *Turdus migratorius*	5	2	3	1	*H. fallisi*, *L. dubreuli*	*H., L., P.*
Swainson's Thrush *Catharus ustulatus*	1	0	0	0		*H., L., P.*
Western Bluebird *Sialia mexicana*	4	0	0	1	*P. relictum*	*L.*
Tyrannidae						
Ash-throated Flycatcher *Myiarchus cinerascens*	8	0	0	0		Negative
Black Phoebe *Sayornis nigricans*	3	0	1	0		*L., P.*
Pacific-slope Flycatcher *Empidonax difficilis*	6	0	0	0		*H., L.*
Western Wood-peewee *Contopus sordidulus*	2	0	0	0		*H., P.*
Troglodytidae						
Bewick's Wren *Thryomanes bewickii*	7	1	0	1	***H.* sp.** *P.* (*Haemamoeba*) sp.	*L.*
Cardinalidae						
Black-headed Grosbeak *Pheucticus melanocephalus*	5	3	3	0	***H. fringillae***	*H., L., P.*
Lazuli Bunting *Passerina amoena*	2	0	1	0	***L. fringillinarum***	*H., L.*
Parulidae						
Black-throated Gray Warbler *Dendroica nigrescens*	4	2	1	0	*H. coatneyi*	*H.*
Orange-crowned Warbler *Vermivora celata*	19	4	1	1	*H. coatneyi*, *L. fringillinarum*	*H., L.*
Yellow-rumped Warbler *Dendroica coronata*	1	0	0	0		*H., L., P.*
Sylviidae						
Blue-gray Gnatcatcher *Polioptila caerulea*	1	0	0	0		*P.*
Certhiidae						
Brown Creeper *Certhia americana*	3	0	0	0		Not sampled
Icteridae						
Bullock's Oriole *Icterus bullockii*	6	2	2	1	*H. quiscalus* *L. fringillinarum*	*H., L., P.*
Red-winged Blackbird *Agelaius phoeniceus*	3	0	0	0		*H., L., P.*
Aegithalidae						
Bushtit *Psaltriparus minimus*	3	2	0	0	Undescribed *H.* sp.	*H.*
Mimidae						
California Thrasher *Toxostoma redivivum*	3	0	0	1		*H., L., P.*

TABLE 1. Continued.

Birds family, common name, taxonomy	*n*	*H.*	*L.*	*P.*	Parasite species	Previous
Vireonidae						
Cassin's Vireo	6	6	0	0	***H. vireonis***	Not sampled
Vireo cassinii						
Hutton's Vireo	3	0	0	0		*H.*
Vireo huttoni						
Warbling Vireo	7	4	0	0	***H. vireonis***	*H., L.*
Vireo gilvus						
Emberizidae						
Chipping Sparrow	2	1	0	0	*H. fringillae*	*H., L., P.*
Spizella passerina						
Dark-eyed Junco	19	11	3	0	*H. fringillae*	*H., L., P*
Junco hyemalis					*L. fringillinarum*	
Fox Sparrow	1	0	0	0		*H., L., P.*
Passerella iliaca						
Golden-crowned Sparrow	6	6	0	0	*H. fringillae*	*H., L., P.*
Zonotrichia atricapilla						
Lark Sparrow	5	5	0	0	*H. fringillae*	*H., P.*
Chondestes grammacus						
California Towhee	6	6	0	2	*H. coatneyi*	*H., L., P.*
Pipilo crissalis						
Rufous-crowned Sparrow	1	0	0	0		*H.*
Aimophila ruficeps						
Sage Sparrow	1	0	0	0		Not sampled
Amphispiza belli						
Song Sparrow	5	1	0	0	*H. fringillae*	*H., L., P.*
Melospiza melodia						
Spotted Towhee	7	7	0	0	*H. fringillae*	*H., L., P.*
Pipilo maculatus						
Fringillidae						
Lesser Goldfinch	47	11	4	0	***H. fringillae***	*H.*
Carduelis psaltria					***L. majoris***	
Purple Finch	9	3	0	0	*H. fringillae*	*H., L., P.*
Carpodacus purpureus						
Paridae						
Oak Titmouse	57	0	14	0	*L. majoris*	*L.*
Baeolophus inornatus						
Corvidae						
Stellar's Jay	3	2	1	0	*H. danilewskii*	*H., L., P.*
Cyanocitta stelleri					*L. berestneffi*	
Western Scrub-jay	2	1	0	1	***H. picae***	*H., L., P.*
Aphelocoma californica					*P.* (*Haemamoeba*) sp.	
Hirundinidae						
Violet-green Swallow	7	5	0	0	*H. hirundinis*	*H., L.*
Tachycineta thalassina						
Thraupidae						
Western Tanager	4	4	1	0	***H. fringillae***	*H., L., P.*
Piranga ludoviciana						
Sittidae						
White-breasted Nuthatch	5	0	0	0		*H., L.*
Sitta carolinensis						
Timaliidae						
Wrentit	16	5	1	1	*H. timalus*	*H., L.*
Chamaea fasciata						
Picidae						
Acorn Woodpecker	10	0	0	0		Negative
Melanerpes formicivorus						
Downy Woodpecker	1	0	0	0		*H.*

TABLE 1. Continued.

Birds family, common name, taxonomy	*n*	*H.*	*L.*	*P.*	Parasite species	Previous
Picoides pubescens						
Northern Flicker	3	0	0	0		*H., L., P.*
Colaptes auratus						
Nuttall's Woodpecker	4	0	0	0		Not sampled
Picoides nuttallii						
Phasianidae						
California Quail	1	1	0	0	***H. lophortyx***	*H.*
Callipepla californica						
Totals	324	96	36	10		

dians ($n=18$). Otherwise, the parasites were broadly distributed among bird families.

Hatching-year birds found infected with *Haemoproteus* spp. include the Bushtit, Song Sparrow (*Melospiza melodia*), Purple Finch (*Carpodacus purpureus*), Western Scrub-jay (*Aphelocoma californica*), Black-headed Grosbeak (*Pheucticus melanocephalus*), Dark-eyed Junco (*Junco hyemalis*), and Wrentit (*Chamaea fasciata*). The Dark-eyed Junco, Black-headed Grosbeak, and Bullock's Oriole (*Icterus bullockii*) were found to be infected with *Leucocytozoon* spp. and the Western Scrub-jay with a *Plasmodium* sp. Thus, transmission likely occurs at the sites for all parasite genera and for a broad diversity of bird species.

Because prevalence of the three parasite genera has been reported to vary with ecologic characteristics of birds, we chose to examine prevalence among host families, assuming that there are fundamental ecologic differences among species in the avian taxonomic families. Sample sizes, however, were large enough to compare only prevalence of *Haemoproteus* spp. among eight bird families: Parulidae (6/24), Tyrannidae (1/19), Vireonidae (10/16), Emberizidae (37/53), Fringillidae (14/56), Paridae (14/56), Timaliidae (5/16), and Picidae (0/18). Contingency tables (infected vs. not infected vs. bird family) demonstrated a significant family effect ($\chi^2=92.8$, df=7, $P<0.0001$). Post hoc tests revealed five of the eight families influenced the deviation from null expectations, Tyrannidae, Vireonidae, Emberizidae, Paridae, and Picidae.

To identify any broadscale interaction among species in the parasite genera, the number of mixed infections was compared with expectations of random association (*predicted under random association=proportion of birds infected with parasites of one genus×proportion infected with parasites of a second genus×total sample size*). Of the infected birds, 17 (10%) carried mixed infections of parasite species of two genera, 11 with *Haemoproteus* spp. and *Leucocytozoon* spp., and 6 with *Haemoproteus* spp. and *Plasmodium* spp. The number of observed mixed infections was very similar to the number expected by chance combinations (χ^2 tests, all $P>0.05$).

DISCUSSION

Hemosporidian parasites were common in the surveyed northern California bird community. Fully 39% of sampled birds were infected with parasites of one or more of the studied genera, with a total of 16 species of parasite. However, examination of single blood smears taken from individual birds presents an underestimate of true prevalence because some infections of these parasites remain at low levels in the blood, and are subpatent upon examination of microscope smears; this is demonstrated by using sensitive molecular assays, such as polymerase chain reaction (PCR) (Perkins et al., 1998). The recent development of molecular techniques to separate subpatent infections using genus-specific restriction enzymes may improve estimates of prev-

alence by parasite genus (Beadell and Fleischer, 2005), but even such methods may underestimate the prevalence of infections with parasites of two or more genera (Valkiunas et al., 2006).

Haemoproteus spp. were by far the most common hemosporidian detected in the birds sampled, approximately twice as common as *Plasmodium* spp. and *Leucocytozoon* spp. infections combined. Such pronounced differences in the relative proportion of the three genera have been observed in other surveys (below), suggesting important differences in transmission biology (such as host and vector behavior and density) among sites (Greiner et al., 1975). For example, blackflies typically require flowing water for larval development, and so *Leucocytozoon* parasites are expected to be present only in regions where such habitats are present. We observed dense populations of blackfly (*Simulium* spp.) larvae in seasonally fast-flowing streams on the field station within a km of the study areas. Indeed, the vectors for all the parasite genera must be present at the HREC site because the finding of infected hatching-year birds indicates transmission takes place there for at least some parasite and host species.

The prevalence of parasites identified as *Haemoproteus* also differed among bird families at our study site. These parasites were rare or absent in the flycatchers, woodpeckers, and titmice, but common in sparrows. Again, this suggests that the vectors may differ in abundance and composition according to different habitats or even microhabitats or their use of bird groups for blood meals (Bennett, 1960). Additionally, certain bird families may be more susceptible to infection by *Haemoproteus* parasites, including those transmitted by the local vectors, perhaps because of host-parasite relations, such as cospeciation or immunocompetence (Greiner et al., 1975).

The frequency of mixed infections with species of two of the parasite genera did not differ from the expected frequency if the parasites associate randomly in birds. This simple analysis, though, presents an uncertain result because no information is available on the proportion of birds that are immune to infection (either physiologically or ecologically because of perching and preening behavior). These birds would inflate the total sample size and could shift the results toward a spurious apparent neutral interaction from an actual negative (competitive) one. This long-known problem makes any such analysis tentative (Cohen, 1973; Schall and Bromwich, 1994).

Several of the parasites identified to species appear to have a broad host range. For example, parasites with morphology consistent with *H. fringillae* were found in birds of four families, the cardinals, sparrows, the fringillid finches, and tanagers. However, any discussion concerning host range in the avian hemosporidians is hindered by problematic identifications to species. Molecular phylogenetic analysis reveals that parasites with identical morphology and consistent with a single species of parasite may represent a clade of species, or even species in distant clades (Martinsen et al., 2006). Fallon et al. (2005) simply abandon any attempt to identify parasites to species and use gene sequences to score parasite lineages for analysis of host ranges. A prudent combination of morphologic identification with gene sequence data and phylogenetic analysis provides the best picture of host range for hemosporidian parasites and reveals that at least some of the parasite species can infect birds of a broad range of systematic families (Krizanauskiene et al., 2006). All our species identifications are based on examination of many parasites from an infection and are consistent with morphology expected for those species, but in light of studies of parasite morphology and gene sequence data (Martinsen et al., 2006, 2007), we offer our morphologic species identifications as only preliminary in revealing the species-level diversity of hemosporidian parasites in the bird community sampled.

Comparison of these results with previous studies reveals similar overall prevalence of hemosporidians in bird communities from high latitudes in Alaska, USA, and Canada (Bennett et al., 1992), central and southern California, USA (Clark and Swinehart, 1966b; Herms et al., 1939), Vermont, USA (Barnard and Blair, 1986), Ontario, Canada (Bennett and Fallis, 1960), southeastern USA (Greiner et al., 1975), central USA (Greiner et al., 1975), and the Lesser Antilles (Apanius et al., 2000; Fallon et al., 2005). Only two surveys reported much lower prevalence, for southern California, USA (3%; Wood and Wood, 1937) and Cape Code, USA (7%; Herman, 1938). *Leucocytozoon* spp. appear to predominate in some northern zones (Vermont, USA; Barnard and Bair, 1986; Ontario, Canada; Bennett and Fallis, 1960). In the Lesser Antilles, *Leucocytozoon* spp. appear absent, and *Plasmodium* spp. predominate (Apanius et al., 2000; Fallon et al., 2005). At all other sites, *Plasmodium* parasites are rare, and *Haemoproteus* spp. predominate (above references). Greiner et al. (1975) suggest that *Leucocytozoon* spp. are rare in central USA because fast-flowing water required for the vector blackflies is relatively scarce. Perhaps, blackflies feeding on birds are also rare in the Caribbean islands, although Gill and Paperna (2005) report that *Leucocytozoon* spp. can be undetectable in birds despite high prevalence when the parasites sequester in blood within visceral organs, perhaps not appearing in the blood except during the transmission season and location.

Variation in the prevalence of parasites within the genera *Plasmodium*, *Leucocytozoon*, and *Haemoproteus* among geographic locations and among bird families could have significance for birds at the population and community level if parasites of these three genera exact different costs to their hosts. *Plasmodium* spp. alone undergoes asexual replication in the blood cells, thus, leading to destruction of blood cells by immune response and potential anemia. However, high parasitemia in blood cells of *Leucocytozoon* and *Haemoproteus* infections occur (Martinsen pers. obs.), and damage to visceral organs can be substantial for parasites of these genera (Atkinson and van Riper, 1991; Gill and Paperna, 2005). Thus, researchers in avian wildlife biology must be aware of the potential importance of hemosporidian parasites for the overall ecology of bird populations, and that the prevalence of hemosporidian genera varies substantially among sites and bird families.

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