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Original Contribution

Prevalence of Blood Parasites in Eastern Versus Western House Finches: Are Eastern Birds Resistant to Infection?

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Abstract: The rapid spread of the bacterial disease, *Mycoplasma gallisepticum* (MG), throughout the introduced range of house finches (*Carpodacus mexicanus*) in eastern North America, compared to its slower spread through the native western range, has puzzled researchers and highlights the need to understand the relative differences in health state of finches from both populations. We conducted a light-microscope survey of hemoparasites in populations of finches from Arizona (within the western range) and from Alabama (within the eastern range), and compared our estimates of prevalence to published reports from house finches sampled in both ranges. Of the 33 Arizona birds examined, we recorded hematozoan infections in 16 (48.5%) individuals, compared to 1 infected Alabama bird out of 30 birds examined (3.3%). Based on independent surveys of seven western North American and five eastern North American populations of house finches the average prevalence of blood parasites in western populations is 38.8% (±17.9 SD), while the average prevalence within the eastern range is only 5.9% (±6.1 SD). The average rate of infection among all songbirds sampled in the east is 34.2% (±4.8 SD). Thus, our surveys of wild birds as well as previously published observations point to eastern house finches having a much lower prevalence of blood parasite infections than their western counterparts. Combined with the fact that eastern finches also tend to have lower rates of avian pox infections than do western birds (based on a literature review), these observations suggest that eastern birds have either strong resistance to these infections or high susceptibility and associated mortality.

Keywords: *Carpodacus mexicanus*, hemoparasites, disease resistance, native, introduced

Introduction

Despite being separated by less than 100 generations, house finches (*Carpodacus mexicanus*) in eastern North America have diverged from their western parent population in a number of ways. Because the entire eastern population was derived from a small number of western birds released around 1940 (Elliott and Arbib 1953), individuals in the eastern population appear to have lower genetic diversity than those in the western population (Hawley et al. 2006). Furthermore, the well-studied epidemic of *Mycoplasma gallisepticum* (MG) infections that began in the mid-1990s (Dhondt et al. 1998) has impacted eastern populations of house finches more than western populations (Dhondt et al. 2006; Hochachka and Dhondt 2000). In fact, the lower genetic diversity of eastern birds was initially thought to be a driving factor in the spread of the disease

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throughout the east (Dhondt et al. 2006), but new evidence from captive studies does not support this idea (Hawley et al. 2010). There are also differences between eastern and western populations in clutch size (Wootton 1986), in metabolic responses to cold (O'Connor 1996), in the size and shape of males and females (Badyaev and Hill 2000), and in migratory behavior (Belthoff and Gauthreaux 1991). Finally, the carotenoid coloration of males averages redder in hue in eastern populations compared to most western populations (Hill 1993a). In the current study we examined differences between eastern and western populations in another trait, the frequency of infection by blood parasites.

There is a long history of research on the blood parasites of North American passerines. Much of the early work involved descriptive surveys of the hemoparasite fauna of birds in certain regions (e.g., Herms et al. 1939; Jordan 1943; Wood and Herman 1943), and projects of this nature are still being conducted (Deviche et al. 2001a; Garvin et al. 1993; Super and Van Riper 1995). These surveys typically involve capturing as many birds as possible (often over many years), examining stained blood films under a microscope for hemoparasites, and reporting their prevalence in each species and region of study. For example, Clark and Swinehart (1966) reported that 34.9% of 23 species of passerines in Sacramento, California were infected with one or more blood parasite types, including species of *Plasmodium*, *Haemoproteus,* and *Leucocytozoon*, which are the most common types of avian blood parasites (Desser and Bennett 1993). In central Vermont, Barnard, and Bair (1986) found 42.5% of over 1,500 birds (50 species) were infected. In a monumental effort, Greiner et al. (1975) assimilated published and unpublished data on hemoparasite prevalence of 57,000 birds from 388 species to make large-scale comparisons of infection prevalence across regions of North America. They concluded that overall hemoparasite prevalence in the western United States was 45% while prevalence in the southeastern states was 35% and in the northeast it was 38%. These reviews, as well as the original reports themselves, continue to be useful resources for evaluating estimates of hemoparasite prevalence in contemporary research projects.

Here we report results from surveys of blood parasite infections using conventional microscopy of stained blood films collected from house finches in western (Arizona) and eastern (Alabama) populations. We combined these new data with information we compiled from the ornithological literature concerning the prevalence of blood parasites in house finches sampled in populations throughout North America. Our findings with both approaches regarding differences in infection prevalence between eastern and western house finches provide novel insights into the relative health of eastern and western House Finches and may hold implications for the spread of *M. gallisepticum* in North America.

Methods

Capturing and Handling House Finches

We captured wild male house finches at backyard feeding stations in Southeast Arizona (AZ). Two teams of biologists captured finches in Green Valley, AZ and Tempe, AZ, respectively, on 11, 12, and 13 August 2010. These collecting sites are 216 km apart but within the same physiographic region occupied by the same subspecies of house finches (Moore 1939). A total of 129 birds from Arizona were sampled, but due to issues with staining of blood films, we could only quantify the parasites on slides from 33 of the Arizona birds. Alabama birds were captured on 1 August 2010 at a single trapping location on the campus of Auburn University, Auburn, Alabama. For all birds sampled, blood was drawn from the brachial vein and a small drop of blood was then spread across a microscope slide following conventional methods for creating blood smears (Houwen 2000).

Blood Smears

Slides from both populations were viewed by a single observer (AKD) with a light microscope under 1,000× (oil) to quantify prevalence of blood parasite infections. Each slide was scanned in a zig-zag pattern (to sample multiple areas of the smear) until 50 fields of view were examined. At this magnification, fields have ~400 erythrocytes (Davis, unpubl. data), so this was equivalent to screening ~20,000 cells per bird. Fields were examined for the presence of common avian parasites, including *Plasmodium*, *Haemoproteus,* and *Leucocytozoon*.

Literature Review

For comparison to our field data of parasitism in house finches from Arizona and Alabama, we compiled published reports of blood parasite prevalence from house finches in other locations in North America, and grouped these into "western" or "eastern" records based on the range of this

species (Hill 1993b). These reports included parasite and health surveys of house finches specifically (i.e., where birds were screened for multiple infections, including blood parasites), and large-scale, multi-species surveys of hematozoa only, of which house finches were examined along with other species. We also noted the overall prevalence of hematozoa reported in the large-scale studies, for comparison with the house finch records. Importantly, all of the studies we compiled used methodology similar to ours (i.e., light microscopy-analysis of stained blood smears).

Results

Prevalance of Blood Parasites

Of the 33 Arizona house finches we examined, we noted hematozoan infections in 16 (48.5%) individuals. All were infections with *Plasmodium* sp., based on the appearance of the organisms (we did not attempt to identify the parasite species). Affected cells contained blue-staining gametocytes of varying size within their cytoplasm (Fig. 1A–E). In cells with large gametocytes, the nucleus was often displaced. Intensity of infections overall was low; of the 16 infected birds, the average number of parasites seen was 2 (±3 SD) in 50 fields of view (~20,000 erythrocytes), or ~0.01% of red blood cells. Of the 30 house finches examined from Alabama, we detected a hematozoan infection in only one individual (3.3%). The parasite appeared to be a *Haemoproteus* sp. based on morphology (Fig. 1F), and again, the infection severity was low; only one parasite was observed in 50 fields of view.

Results of Literature Review

We compiled a total of 12 published accounts (including one unpublished thesis) in which blood smears from house finches were examined for hematozoa (Table 1). There were five records from the eastern range of the house finch (plus our estimate from the Alabama birds), and seven studies from the western range (plus our results from the Arizona birds). The prevalence of blood parasite infection in the Arizona house finches (48.5%) was generally consistent with reports from other locations within the western range; the average prevalence of all western reports (besides ours) was 38.8% (±17.9 SD). The western average *including* the Arizona birds was 40.0% (±17.0 SD). Similarly, the low prevalence of blood parasite infection in our sample of Alabama house finches (3.3%) was consistent with those from elsewhere in the eastern range, where the overall average was 5.5% (±5.6 SD) and ranged from 0.0 to 16.2% (Table 1).

A statistical comparison of prevalence estimates from Table 1 indicated the average prevalence within the eastern range was significantly different from the western average (Student's *t*-test, df = 12, $t = -4.74$, $P = 0.0005$). Because the sample sizes varied in the studies in Table 1, we performed this test a second time after weighting the records using a 1–3 score, based on the sample size of the study

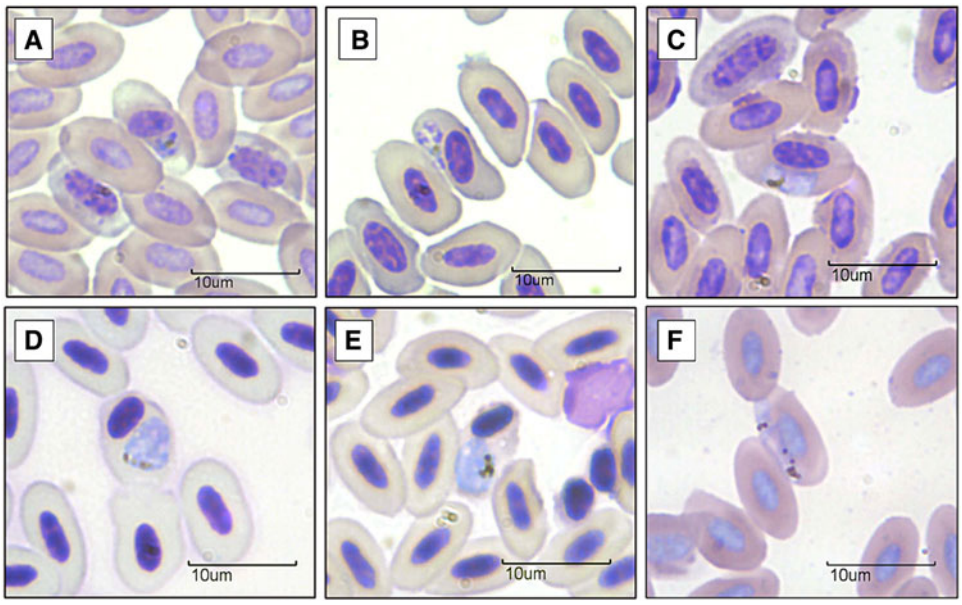

Figure 1. Photomicrographs of blood parasites observed in house finches from Arizona (*Plasmodium* sp., **A–E**) and Alabama (*Hemoproteus* sp., **F**).

Table 1. Summary of Published Studies Where House Finches were Examined for Hematozoa Using Light Microscopy, for Comparison with Data from the Current Study (Shown in Bold).

Region	Location	# Birds examined	% Infected	Sample effort	Source
East	Oklahoma	34	5.8	1	Bay and Andrews (2009)
East	Ohio	416	0.0	2	Morishita et al. (1999)
East	Georgia	757	16.2	3	Hartup et al. (2008)
East	New York	282	4.6	2	Hartup et al. (2008)
East	Wisconsin	305	3.0	2	Hartup et al. (2004)
East	**Alabama**	**30**	**3.3**	**1**	**This study**
West	California	530	13.0	3	Wood and Herman (1943)
West	Colorado	10	50.0	1	Stabler and Kitzmiller (1970)
West	California	51	56.8	1	Thakur (1998)
West	Mexico City	61	37.7	1	Hewitt (1940)
West	California	8	25.0	1	Clark and Swinehart (1966)
West	California	39	61.5	1	Herms et al. (1939)
West	California	1,741	27.8	3	Herman et al. (1954)
West	**Arizona**	**33**	**48.5**	**1**	**This study**

Sample effort was a code assigned to each study and used for weighting purposes

Table 2. Summary of Published Studies Where Large-Scale, Multi-Species Surveys of Avian Hematozoa were Conducted, Using Light Microscopy.

Region	Location	# Birds examined	% Infected	# Species examined	Source
East	Northeast Georgia	1,091	30.4	13	Jordan (1943)
East	Southwest Georgia	1,068	30.1	50	Love et al. (1953)
East	New Jersey	697	29.3	59	Kirkpatrick and Suthers (1988)
East	"Region 1'"(southeastern US)	6,569	35.0	>100	Greiner et al. (1975)
East	"Region 5" (northeastern US)	30,549	38.0	>100	Greiner et al. (1975)
East	Vermont	1,547	42.5	50	Barnard and Bair (1986)
East	Louisiana	935	34.2	19	Garvin et al. (1993)
West	California	1,525	23.4	112	Wood and Herman (1943)
West	California	150	27.3	30	Herms et al. (1939)
West	California	383	34.9	23	Clark and Swinehart (1966)
West	"Region 3" (western US)	8,784	45.0	>100	Greiner et al. (1975)
West	California	1,028	22.9	40	Super and Van Riper (1995)
West	Vancouver Is. British Columbia	197	35.0	29	Williams (1978)

(1–100 = 1, 101–500 = 2, >501 = 3). This did not change the outcome of this comparison (df = 21, $t = -4.86$, $P < 0.0001$). The low prevalence of the eastern house finches was even more interesting when compared to the published reports of multi-species surveys (Table 2). Across the eastern region of North America, the average prevalence of avian hematozoa was 34.2% (±4.8 SD). In the western region it was 31.4% (±8.5 SD), and these means were not significantly different (df = 11, $t = 0.74$, $P = 0.472$). Furthermore, the average prevalence of hematozoa in western house finches was not different than the average prevalence of all other birds (df = 12, $t = 1.13$, $P = 0.279$), while in the east, the house finch average was significantly lower than the average of all other birds (df = 11, $t = -9.9$, $P < 0.0001$). In sum, the frequency of blood parasite infections of house finches in the east appears to be about eight times less than in western house finches and about seven times less than other birds in the eastern United States (Fig. 2).

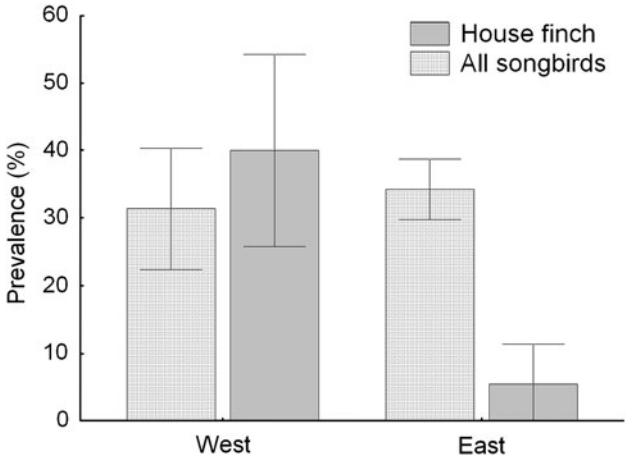

Figure 2. Average prevalence of hemoparasites in house finches and other songbirds from western and eastern North America, based on data summarized in Tables 1 and 2. *Error bars* represent 95% confidence intervals.

Discussion

In this project we used both our own field surveys and a literature review to compare the prevalence of blood parasite in eastern and western house finches. Both methods pointed to introduced eastern finches having considerably lower rates of infections than their native western counterparts. We cannot easily attribute the lower incidence of blood parasites to differences in exposure to possible vectors because, when we compared the prevalence in the infection rates in eastern and western North America for all passerine species, the rates of infection were not significantly different: 34.2 vs. 31.4%. Thus, house finches in the native range appear to have similar rates of infection as other passerine species while house finches in the east have lower rates of infection than most other birds in this region (Fig. 2).

We are confident in the results of this investigation for two reasons. First, our own field surveys of populations of eastern and western house finches utilized the same method for detecting hemoparasites for both populations: blood smear analyses that were conducted by the same observer using a standardized procedure. Moreover, the house finches in both populations were captured using similar techniques and during the summer (in fact the same month—August) when prevalence of vector-borne hemoparasites should be high (Barnard and Bair 1986; Deviche et al. 2001b; Super and Van Riper 1995). Second, our results were consistent with those from multiple independent surveys (five from the east, seven from the west, Table 1) that also used microscopic detection to estimate parasite prevalence.

Interestingly, the geographic pattern in hemoparasite prevalence that we report is not consistent with a prior investigation of hematozoa in house finches where molecular markers (polymerase chain reaction, PCR) were employed to identify specific parasite species across North America (Kimura et al. 2006). In that study, average prevalence of hemoparasites in three populations of eastern house finches (in New York, Georgia and Wisconsin) was 32%, while the average of five western populations (South Dakota, California, Idaho, Arizona and Nevada) was 43.8%. This discrepancy between our two results likely stems from the inherent differences in detection ability of conventional microscopy versus PCR-based approaches to diagnose hemoparasite infections (Garamszegi 2010). Molecular tools are generally considered to be more effective than microscopy (but see Jarvi et al. 2002). They can detect infections even when parasitemia (infection intensity) is very low, while such infections may be missed in routine scanning of blood smears. Thus, it is possible that the "low prevalence" of hematozoa that we observed in eastern house finches was actually a reflection of low intensity of infection in many birds in this population, compared to those in the west. Low-intensity infections could have been missed in the investigations of eastern finches, where light microscopy was used. By employing PCR-based detection of hemoparasites, Kimura et al (2006) would have been able to detect such low-intensity infections in this population.

The differences in geographic prevalence found here as compared to the Kimura et al. (2006) study draw attention to a larger issue, that is the biological relevance of infections detected using molecular-based tools versus microscopic detection (e.g., Kriger et al. 2007; Smith 2007). Since molecular methods can detect extremely minute infections, one wonders how important these infections would be to the host than those that are severe enough to be detected using light microscopy. In fact, in a recent study directly comparing methodologies, Nayel et al. (2012) concluded that microscopy is a more appropriate tool for detecting acute infections while molecular methods are better-suited for detecting chronic, "subclinical" infections. Future studies should be aimed at examining effects of acute versus chronic (or subclinical) hemoparasite infections, which would help to resolve this issue of biological relevance.

The frequency of hemoparasite infections in western and eastern house finches is particularly interesting considering the geographic patterns in another well-known pathogen of this (and other passerine) species: avian pox. This is a disease characterized by visible, wart-like lesions on the head, wings, and legs (Bolte et al. 1999; McClure 1989) and is often reported by bird-banders and ornithologists. Based on our own review of this literature we determined the prevalence of pox in western house finches is ~20% (McClure 1989; Power and Human 1976; Spears and Cavitt 2003; Zahn and Rothstein 1999). Meanwhile, independent surveys of eastern finches all show that less than 5% of birds have pox lesions (Davis 2010; Hartup et al. 2004; Zahn and Rothstein 1999, GEH personal observation). These observations of pox infections provide another example of lower disease prevalence in the introduced house finch population, and engender further questions regarding the resistance of eastern house finches to these and other infections. Moreover, these geographic patterns in prevalence of hematozoan and pox are different than the patterns of prevalence observed for MG, which spread rapidly through the eastern range of house finches but has spread relatively slowly through western populations (Dhondt et al. 2005).

Recent projects with captive house finches have advanced our understanding of the MG pathogen and its geographic variation in prevalence. Hawley et al (2010) conducted experimental infection experiments with eastern and western house finches to test whether the faster spread and greater intensity of MG infections in eastern house finches compared to western finches was caused by lower genetic heterogeneity of eastern birds, which was once widely-thought to be the case (Dhondt et al. 2005, 2006; Hawley et al. 2005, 2006). Results from that project showed that the geographic variation in MG prevalence appears to be influenced less by host genetic diversity and more by variation in the pathogen itself, which is less virulent in the western range (Hawley et al. 2010). Another experimental study also showed lower pathogenicity (less severe eye lesions, lower pathogen load, and lower levels of antibodies) in a western strain of MG compared to that of eastern strains (Grodio et al. 2012). In an experimental infection experiment in which eastern and western house finches were inoculated with the same strain of MG, eastern birds showed greater resistance to mycoplasmosis (Bonneaud et al. 2011). Thus, the pattern of MG prevalence seems to be a consequence of geographic variation in both bacterial pathogenicity and host resistance.

Besides a possible difference in infection severity, what else could explain the exceptionally low prevalence of blood parasites in eastern house finches, especially compared to other birds in this region? One possibility is that this is an example of the enemy release hypothesis, which argues that organisms introduced into novel environments experience greater success because of the release from naturally co-evolved parasites present in the native range (Lima et al. 2010; Marzal et al. 2011). Kimura et al (2006) determined that eastern finches carry different strains of plasmodium parasites than their western counterparts. It may be that the particular combination of strains in the east is less virulent (i.e., does not transmit efficiently, or hosts can more easily clear the infection). Testing this hypothesis would require experimentally testing pathogen clearance rates under controlled (captive) conditions.

A second explanation is that eastern house finches may in fact be *highly* susceptible to hemoparasites, and that infected individuals (especially young birds) are selectively removed from the population that is sampled in parasite screening investigations (i.e., ''selective mortality''). This would lead to the appearance of low infection prevalence in a population. Moreover, one could argue that the high prevalence of MG in the eastern population could in theory contribute to this, since birds with MG-infections show reduced defensive behaviors toward mosquitoes (Darbro et al. 2007), which could in turn lead to increased susceptibility of MG-infected birds to hemoparasite infections. However, field data from a prior study of (eastern) house finches in Atlanta, GA does not support this idea; of 159 birds captured between August 2001 through February 2002 (the time of year when MG prevalence is high), 21% of birds with no MG symptoms had blood parasites, while 26% of birds with MG symptoms did, and the frequencies were not significantly different, based on a chi-square analysis ($\chi^2 = 0.612$, $P = 0.434$; Davis, unpubl. data). Thus, since there is no evidence that MG infections lead to greater incidence of hemoparasite infections, it stands to reason that MG is not contributing (at least directly) to the low frequency of hemoparasite infections in eastern house finches. Two independent studies also found little evidence for hemoparasite-induced selective-mortality in other bird populations (Knutie et al. 2012; Sol et al. 2003).

Finally, we point out that the results from this work highlight the value of combining novel empirical studies with assessment of published surveys. Here, we uncovered a pattern that may have bearing on many current research projects focusing on the house finch-MG system based

largely on information that has been in the published literature for many years. Our results also demonstrate the continued usefulness of the early descriptive studies of avian hematozoa that were conducted even seven decades ago.

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References

Badyaev AV, Hill GE (2000) The evolution of sexual dimorphism in the house finch. I. Population divergence in morphological covariance structure. *Evolution* 54:1784–1794

Barnard WH, Bair RD (1986) Prevalence of avian hematozoa in central Vermont. *Journal of Wildlife Diseases* 22:365–374

Bay MD, Andrews KD (2009) Prevalence of hematozoan parasites (apicomplexa) in some common passerine birds (Passeriformes) from east-central Oklahoma. *The Texas Journal of Science* 61:311–318

Belthoff JR, Gauthreaux SA (1991) Partial migration and differential winter distribution of House Finches in the eastern United States. *Condor* 93:374–382

Bolte AL, Meurer J, Kaleta EF (1999) Avian host spectrum of avipoxviruses. *Avian Pathology* 28:415–432

Bonneaud C, Balenger SL, Russell AF, Zhang JW, Hill GE, Edwards SV (2011) Rapid evolution of disease resistance is accompanied by functional changes in gene expression in a wild bird. *Proceedings of the National Academy of Sciences of the United States of America* 108:7866–7871

Clark GW, Swinehart B (1966) Blood protozoa of passerine birds of the Sacramento (Calif.) region. *Journal of Wildlife Diseases* 2:53–54

Darbro JM, Dhondt AA, Verrneylen FM, Harrington LC (2007) *Mycoplasma gallisepticum* infection in house finches (*Carpodacus mexicanus*) affects mosquito blood feeding patterns. *American Journal of Tropical Medicine and Hygiene* 77:488–494

Davis AK (2010) Mycoplasmal conjunctivitis in house finches (*Carpodacus mexicanus*) is more severe in left eyes than right. *Avian Biology Research* 3:153–156

Desser SS, Bennett GF (1993) The parasitic Leucocytozoon, Haemoproteus and Hepatocystis. In: *Parasitic Protozoa*, Vol 4, Kreier JP (editor), *2nd ed.* New York, NY: Academic Press, pp 273–307

Deviche P, Greiner EC, Manteca X (2001) Interspecific variability of prevalence in blood parasites of adult passerine birds during the breeding season in Alaska. *Journal of Wildlife Diseases* 37:28–35

Deviche P, Greiner EC, Manteca X (2001) Seasonal and age-related changes in blood parasite prevalence in Dark-eyed Juncos (*Junco hyemalis*, Aves, Passeriformes). *Journal of Experimental Zoology* 289:456–466

Dhondt AA, Tessaglia DL, Slothower RL (1998) Epidemic mycoplasmal conjunctivitis in house finches from eastern North America. *Journal of Wildlife Diseases* 34:265–280

Dhondt AA, et al. (2005) Dynamics of a novel pathogen in an avian host: mycoplasmal conjunctivitis in house finches. *Acta Tropica* 94:77–93

Dhondt AA, et al. (2006) Dynamics of mycoplasmal conjunctivitis in the native and introduced range of the host. *EcoHealth* 3:95–102

Elliott JJ, Arbib RS (1953) Origin and status of the house finch in the eastern United States. *Auk* 70:31–37

Garamszegi LZ (2010) The sensitivity of microscopy and PCR-based detection methods affecting estimates of prevalence of blood parasites in birds. *Journal of Parasitology* 96:1197–1203

Garvin MC, Remsen JV, Bishop MA, Bennett GF (1993) Hematozoa from passeriform birds in Louisiana. *Journal of Parasitology* 79:318–321

Greiner EC, Bennett GF, White EM, Coombs RF (1975) Distribution of the avian hematozoa of North America. *Canadian Journal of Zoology* 53:1762–1787

Grodio JL, et al. (2012) Pathogenicity and immunogenicity of three *Mycoplasma gallisepticum* isolates in house finches (*Carpodacus mexicanus*). *Veterinary Microbiology* 155:53–61

Hartup BK, Stott-Messick B, Guzy M, Ley DH (2004) Health survey of house finches (*Carpodacus mexicanus*) from Wisconsin. *Avian Diseases* 48:84–90

Hartup BK, Oberc A, Stott-Messick B, Davis AK, Swarthout ECH (2008) Blood parasites of house finches (*Carpodacus mexicanus*) from Georgia and New York. *Journal of Wildlife Diseases* 44:469–474

Hawley DM, Sydenstricker KV, Kollias GV, Dhondt AA (2005) Genetic diversity predicts pathogen resistance and cell-mediated immunocompetence in house finches. *Biology Letters* 1:326–329

Hawley DM, Hanley D, Dhondt AA, Lovette IJ (2006) Molecular evidence for a founder effect in invasive house finch (*Carpodacus mexicanus*) populations experiencing an emergent disease epidemic. *Molecular Ecology* 15:263–275

Hawley DM, et al. (2010) Common garden experiment reveals pathogen isolate but no host genetic diversity effect on the dynamics of an emerging wildlife disease. *Journal of Evolutionary Biology* 23:1680–1688

Herman CM, Reeves WC, McClure HE, French EM, Hammon WM (1954) Studies on avian malaria in vectors and hosts of encephalitis in Kern County, California. *American Journal of Tropical Medicine and Hygiene* 3:676–695

Herms WB, Kadner CG, Galindo P, Armstrong DF (1939) Blood parasites of California birds. *Journal of Parasitology* 25:511–512

Hewitt R (1940) Studies on blood protozoa obtained from Mexican wild birds. *Journal of Parasitology* 26:287–295

Hill GE (1993) Geographic variation in the carotenoid plumage pigmentation of male house finches (*Carpodacus mexicanus*). *Biological Journal of the Linnean Society* 49:63–86

Hill GE (1993b) House finch (*Carpodacus mexicanus*). In: *The Birds of North America. Number 46*. Philadelphia: The Academy of Natural Sciences

Hochachka WM, Dhondt AA (2000) Density-dependent decline of host abundance resulting from a new infectious disease. *Proceedings of the National Academy of Sciences* 97:5303–5306

Houwen B (2000) Blood film preparation and staining procedures. *Laboratory Hematology* 6:1–7

Jarvi SI, Schultz JJ, Atkinson CT (2002) PCR diagnostics underestimate the prevalence of avian malaria (*Plasmodium relictum*) in experimentally-infected passerines. *Journal of Parasitology* 88:153–158

Jordan HB (1943) Blood protozoa of birds trapped at Athens, Georgia. *Journal of Parasitology* 29:260–263

Kimura M, Dhondt AA, Lovette IJ (2006) Phylogeographic structuring of *Plasmodium* lineages across the north american range of the house finch (*Carpodacus mexicanus*). *Journal of Parasitology* 92:1043–1049

Kirkpatrick CE, Suthers HB (1988) Epizootiology of blood parasite infections in passerine birds from central New Jersey. *Canadian Journal of Zoology-Revue Canadienne De Zoologie* 66:2374–2382

Knutie SA, Waite JL, Clayton DH (2012) Does avian malaria reduce fledging success: an experimental test of the selection hypothesis. *Evolutionary Ecology*. Online first (DOI:10.1007/s10682-012-9578-y)

Kriger KM, Ashton KJ, Hines HB, Hero JM (2007) On the biological relevance of a single *Batrachochytrium dendrobatidis* zoospore: a reply to Smith (2007). *Diseases of Aquatic Organisms* 73:257–260

Lima MR, Simpson L, Fecchio A, Kyaw CM (2010) Low prevalence of haemosporidian parasites in the introduced house sparrow (*Passer domesticus*) in Brazil. *Acta Parasitologica* 55:297–303

Love GJ, Wilkin SA, Goodwin MHJ (1953) Incidence of blood parasites in birds collected in southwestern Georgia. *Journal of Parasitology* 39:52–57

Marzal A, et al. (2011) Diversity, loss, and gain of malaria parasites in a globally invasive bird. *Plos One* 6:8

McClure HE (1989) Epizootic lesions of house finches in Ventura County, California. *Journal of Field Ornithology* 60:421–430

Moore RT (1939) A review of the house finches of the subgenus *Burrica*. *Condor* 41:177–205

Morishita TY, Aye PP, Ley EC, Harr BS (1999) Survey of pathogens and blood parasites in free-living passerines. *Avian Diseases* 43:549–552

Nayel M, et al. (2012) The use of different diagnostic tools for *Babesia* and *Theileria* parasites in cattle in Menofia, Egypt. *Parasitology Research* 111:1019–1024

O'Connor TP (1996) Geographic variation in metabolic seasonal acclimatization in house finches. *Condor* 98:371–381

Power DM, Human G (1976) A local occurrence of avian pox in the house finch. *Condor* 78:262–263

Smith KG (2007) Use of quantitative PCR assay for amphibian chytrid detection: comment on Kriger et al. (2006a,b). *Diseases of Aquatic Organisms* 73:253–255

Sol D, Jovani R, Torres J (2003) Parasite mediated mortality and host immune response explain age-related differences in blood parasitism in birds. *Oecologia* 135:542–547

Spears L, Cavitt JF (2003) The prevalence and effect of avian pox on body condition and plumage coloration in northern populations of House Finches. *Utah Birds* 17:25–33

Stabler RM, Kitzmiller N (1970) Hematozoa from Colorado birds. III. Passeriformes. *Journal of Parasitology* 56:12–16

Super PE, Van Riper C (1995) A comparison of avian hematozoan epizootiology in two California coastal scrub communities. *Journal of Wildlife Diseases* 31:447–461

Thakur S (1998) Effect of high temperatures and crowding on leukocyte and parasite counts of the house finch (*Carpodacus mexicanus*). Unpublished Masters Thesis, California State University.

Williams NA (1978) Hematozoa of wild birds from British Columbia. *Journal of Parasitology* 64:556–558

Wood SF, Herman CM (1943) The occurrence of blood parasites in birds from southwestern United States. *Journal of Parasitology* 29:187–196

Wootton JT (1986) Clutch-size differences in western and introduced eastern populations of house finches: patterns and hypotheses. *Wilson Bulletin* 98:459–462

Zahn SN, Rothstein SI (1999) Recent increase in male house finch plumage variation and its possible relationship to avian pox disease. *Auk* 116:35–44