Journal of Wildlife Diseases, 41(3), 2005, pp. 532–541

INTERSPECIFIC DIFFERENCES IN HEMATOZOAN INFECTION IN SONORAN DESERT *AIMOPHILA* SPARROWS

Pierre Deviche,[1,3] Kevin McGraw,[1] and Ellis C. Greiner[2]

[1] School of Life Sciences, Arizona State University, Tempe, Arizona 85287-4501, USA
[2] Department of Pathobiology, College of Veterinary Medicine, Box 110880, University of Florida, Gainesville, Florida 32611, USA
[3] Corresponding author (email: deviche@asu.edu)

ABSTRACT: Numerous studies have identified factors that control avian hematozoan infections, but the mechanisms that account for host differences in parasitemia remain largely speculative. To address this issue, we compared the prevalence of these parasites in stained blood smears from four conspecific Sonoran desert *Aimophila* sparrow species sampled during their breeding season: rufous-winged (*Aimophila carpalis*; RWSP), rufous-crowned (*Aimophila ruficeps*; RCSP), Cassin's (*Aimophila cassinii,* CASP), and Botteri's (*Aimophila botterii*; BOSP) sparrows. Blood smears contained *Haemoproteus fringillae* (RWSP), *Trypanosoma everetti* (RWSP, RCSP, BOSP), *Trypanosoma avium* (CASP), and microfilariae (all species). Most (92.5%) RWSP ($n=40$) were infected with *Haemoproteus,* but this parasite was not detected in RCSP ($n=20$) or BOSP ($n=20$) and was found only in one (2.5%) CASP ($n=40$). *Trypanosoma* spp. and microfilariae were detected in all species, but prevalence differed between these four sparrow species. Species differences in parasite prevalence were not due to difference in sex, age, adult body mass, incubation period, breeding habitat, or plumage colorfulness. However, differences in *Haemoproteus* sp. prevalence correlated with preferred nesting height, as RWSP generally nest above ground, whereas the other species nest on or close to the ground. Elevated *H. fringillae* prevalence in breeding-condition RWSP presumably does not result from a seasonal relapse associated with breeding or require new infection because 1) this prevalence did not differ in males sampled during and outside ($n=21$) the breeding season, and 2) all male RWSP ($n=25$) that we held in captivity and shielded from new infections and influence of natural photoperiod for 1 yr had viable blood *H. fringillae* gametocytes. *H. fringillae* prevalence in fall-sampled hatch-year male RWSP ($n=11$) was 63.6%, demonstrating that this parasite can be transmitted on the breeding grounds and during the first months of life. *T. everetti* prevalence in RWSP was lower in winter than in summer and also in long-term captive than in free-ranging adults. Presence of this parasite in the blood of breeding males may depend on recrudescence of existing infections or new infections.

Key words: Botteri's sparrow, Cassin's sparrow, *Haemoproteus*, microfilariae, rufous-crowned sparrow, rufous-winged sparrow, *Trypanosoma*.

INTRODUCTION

Many studies have described avian hematozoan infections (Bennett and Fallis, 1960; Greiner et al., 1975; Kucera, 1981; Rodriguez and Matta, 2001; Murata, 2002), but the mechanisms that control intra- and interspecific differences in these infections remain poorly understood. Within species, infections vary as a function of age (Godfrey et al., 1990; Seutin, 1994; Deviche et al., 2001a), sex (Weatherhead et al., 1991; Weatherhead and Bennett, 1992; Norris et al., 1994), and behavior and reproductive effort (Nordling et al., 1998). Between as well as within species, infection also is influenced by the host susceptibility (Adriano and Cordeiro, 2001), which itself reflects both host immunity and behavioral factors affecting the likelihood of infection (Scheuerlein and Ricklefs, 2004). Differences in parasite infections have in some studies been associated with differences in body mass, but the nature of this association and the mechanisms involved remain largely speculative (Scheuerlein and Ricklefs, 2004). Finally, infection can depend on characteristics of vectors such as time of emergence and ecological requirements (Cardona et al., 2002; Garvin et al., 2003). These characteristics may account for geographic and between-habitat differences in parasite infections (Merilä et al., 1995; Tella et al., 1999).

To better understand the regulation of avian hematozoan infections, we measured the prevalence of these parasites in four congeneric Sonoran desert sparrow species: rufous-winged, *Aimophila carpalis* (RWSP), rufous-crowned, *Aimophila ruficeps* (RCSP), Cassin's, *Aimophila cassinii* (CASP), and Botteri's, *Aimophila botterii* (BOSP) sparrows. These species are of particular interest for investigating this topic because they share many biological characteristics (Webb and Bock, 1996; Collins, 1999; Dunning et al., 1999; Lowther et al., 1999). For example, they have approximately the same adult body mass (15–20 g) and breed in generally similar (open arid grasslands with low trees and scattered shrubs) and overlapping habitats. In addition, their reproductive season is temporally flexible and coincides with irregular local precipitations. They also have similar incubation periods (11–13 days). These factors in other species have been associated with differences in parasitemia (see above; Ricklefs, 1992; Scheuerlein and Ricklefs, 2004).

Hamilton and Zuk (1982) hypothesized that sexually selected ornamental traits, in particular plumage, constitute reliable signals of resistance to parasites. According to this hypothesis, which remains a matter of considerable debate (Yezerinac and Weatherhead, 1995; Bortolotti et al., 1996; Lindström and Lundström, 2000), expression of these traits across species should be positively associated with susceptibility to parasite infections (Møller, 1990). The four *Aimophila* species that we investigated are not brightly colored to the human eye, yet exhibit species-specific plumages. To evaluate a potential contribution of plumage to parasite infections, we measured plumage colorfulness and examined whether species differences in this parameter parallel differences in parasite prevalence. We also investigated whether differences in prevalence are associated with preferred nesting sites. Research on non-desert forest birds reported parasitemia to be positively related to the vertical stratification of nesting sites (Bennett and Fallis, 1960; Greiner et al., 1975; Garvin and Remsen, 1997). Three sparrow species that we investigated (RCSP, CASP, and BOSP) nest on or close to the ground, but RWSP generally build nests in bushes 0.5–3 m above ground. If parasite vectors in the Sonoran desert are stratified, as is the case in other environments, we hypothesized that RWSP would have a higher parasite prevalence than RCSP, CASP, and BOSP.

To ensure that data were as comparable as possible, we sampled birds that were of same sex (males) and age (adults), were in breeding condition, and were caught in the same region (see Results). To better understand the mechanisms that control parasite prevalence, we determined prevalence in RWSP that we held captive for 1 yr. While captive, these birds were shielded from parasite vectors and the influence of natural photoperiod on relapse induction. We also measured prevalence in males sampled outside the breeding season and in young male RWSP to determine whether these birds can be infected within months of hatching, as is the case for other species (Barnard and Bair, 1986; Weatherhead and Bennett, 1992; Merino and Potti, 1995).

MATERIALS AND METHODS

Free-ranging birds

To compare parasite infections between species and, for RWSP, between adult and hatch-year (HY) males, we caught sparrows in Pima, Santa Cruz, and Cochise counties, Arizona (average latitude and longitude: 31°50'N, 111°NW), using conspecific playback recordings and Japanese mist nets. Adults in breeding condition were caught in July and August 2003 and 2004. Hatch-year male RWSP were caught in summer and fall 2000 and 2001. Male RWSP used for the fall/winter sample were caught in 2000, early 2001, and 2002. Inclusive (in parentheses) and median (in brackets) dates of collection for summer adults were: RWSP (10 July–27 August 2003 [18 July 2003]); RCSP (11 July–28 August 2003 and 2004 [1 August 2003, $n=14$, and 20 August 2004, $n=6$]); CASP (July 24–22 August 2003 and 2004 [15 August 2003, $n=37$, 12 August 2004, $n=3$]); and BOSP (24

July–12 August 2003 and 2004 [24 July 2003, $n=1$; 29 July 2004, $n=19$]). For HY RWSP, dates of collection were 16 August–11 November 2000 and 2001 [7 October 2000; 16 August 2001] and for fall/winter RWSP dates of collection were 11 November–11 January 2000–01 and 2001–02 [11 November 2000; 11 January 2001; 3 December 2002].

To determine whether parasite prevalence in RWSP differs between years and sites, we compared this prevalence in different adult males caught at the same site (site 1: Santa Rita Experimental Range, 31°47'29"N; 110°51'43"W) in 2000 (12 July–10 August, $n=13$) and 2001 (all on 19 July, $n=10$), and at a second site (site 2: Duval Mine, 31°51'25"N; 111°0'45"W) in 2003 (18–31 July, $n=13$). Site 1 is located 8 km from site 2 and most RWSP used in the present investigation were caught within 10 km of these sites.

All captures took place between 5:00 AM and 6:30 PM (Pacific standard time). We determined the sex of all birds either by unilateral laparotomy under lidocaine-induced topical anesthesia and visual inspection of the gonads or, in summer, using external morphologic characteristics (developed cloacal protuberance in males; incubation patch in females; Pyle, 1997). Age (HY or after HY) was determined on the basis of the degree of skull pneumatization (Pyle, 1997). The skull of HY RWSP was largely unpneumatized (median degree of pneumatization = 1 on a scale ranging from 0 [no pneumatization] to 3 [full pneumatization]), indicating that these males were a few months old when captured. The skulls of most male RWSP caught during November through January were completely pneumatized and these birds were, therefore, of unknown age.

Within three minutes of capture, we removed birds from the net and collected blood from the brachial vein into heparinized microhematocrit tubes. We used approximately 5 μl of blood to prepare thin smears on glass microscope slides (Bennett, 1970; Deviche et al., 2001a); blood smears were dried at ambient temperature and were placed in airtight boxes until returned to the laboratory. We then weighed birds to the nearest 0.1 g, marked them with a numbered aluminum leg band, and either released them at the capture site or brought them into captivity. In the laboratory, blood smears were fixed for 5–10 min in absolute methanol and stained using the Giemsa technique (Bennett, 1970). Stained smears were dehydrated overnight under vacuum, cleared with xylene, and covered with 0.16-mm-thick glass coverslips using Cytoseal 60 (VWR, San Francisco, California). The coverslip thickness made it possible to study smears at high (1000×) light microscope magnification under oil immersion for parasite identification. Prevalence of parasites (proportion of infected individuals in a given sample) was determined by light microscopy; one stained blood smear from each bird was viewed for at least 10 min at low (250×) and high (400×) magnification as described by Deviche et al. (2001a). Parasites were identified at 1000× magnification. Representative positive slides from the four sparrow species were deposited at the US National Parasite Collection (Beltsville, Maryland; accession numbers: USNPC 96-450 to -458).

Captive birds

We caught 25 adult male RWSP between 3 July and 14 August 2003, brought them into captivity at the Arizona State University Animal Care Facility, and placed them in light- and temperature-controlled vector-free environmental chambers. Each sparrow was kept in an individual cage and was in visual and acoustic, but not physical, contact with other birds. Sparrows were fed commercial finch chow and received water ad libitum. Twice a week (except 14 April–16 July) they also received live mealworms. Between August 2003 and July 2004, we used these birds for studies on the photoperiodic control of reproduction. During this period we exposed them to specific light regimes and repeatedly bled, measured, and laparotomized them (Deviche and Small, unpubl. data), but they received no other experimental treatment. On 19 July 2004, when males had been captive for approximately 1 yr, a blood smear was obtained for each bird as previously described.

To evaluate the viability of *Haemoproteus fringillae* gametocytes present in the blood of captive RWSP, a blood sample was collected from the brachial vein of five males on 27 July 2004. Blood was dispensed (within seconds of collection) on four microscope slides that we placed in a humid chamber. Two, 3, 4, or 5 min later we spread and air-dried the blood in preparation for staining as described above. Stained smears were studied under the microscope at 400× magnification for the presence of extracellular gametocytes, exflagellating bodies, and free gametes. We assumed that if *H. fringillae* gametocytes became senescent, they would not be able to produce gametes, as reflected by their inability to undergo exflagellation.

Plumage colorfulness

We measured the plumage colorfulness of the four study species ($n=8$ nonmolting adult males per species except BOSP, $n=1$ nonmolting adult male). Because ultraviolet signals

TABLE 1. Body mass and blood parasite prevalence of free-ranging adult male *Aimophila* sparrows in breeding condition.

Species	n	Body mass[a]	Parasite prevalence (% infected birds)			
			Haemoproteus	Microfilariae	*Trypanosoma*	Overall
Rufous-winged sparrow *Aimophila carpalis*	40	15.5±0.8	92.5[b]	2.5	27.5[d]	92.5
Rufous-crowned sparrow *Aimophila ruficeps*	20	19.6±1.1	0	30	15[d]	45
Cassin's sparrow *Aimophila cassinii*	40	17.8±1.0	2.5[c]	2.5	15[e]	17.5
Botteri's sparrow *Aimophila botterii*	20	20.5±1.0	0	5	5[d]	10

[a] Grams, means±standard deviations.
[b] *Haemoproteus fringilliae*.
[c] *Haemoproteus sp.*
[d] *Trypanosoma everetti*.
[e] *Trypanosoma avium*.

were not detected from the body plumage using an Ocean Optics spectrophotometer (Duredin, Florida) as described by McGraw et al. (2002), we measured plumage color using digital photography, which detects only visible light. Each sparrow was photographed twice using a Canon Digital Rebel camera (Elk Grove Village, Illinois) equipped with a Canon EFS 18–55 mm lens. Males were held 21 cm from the camera lens against a standard grayboard background, and the left side of the body was photographed using the built-in camera flash at a shutter speed of 1/60 sec and an aperture value of *f*5.6. Photos were imported into Adobe Photoshop® CS (v. 8.0) (San Jose, California) at an image resolution of 3,072 × 2,048 pixels. Since we were interested in overall colorfulness, we selected the entire lateral profile of each bird with the lasso tool and used red/blue/green values from the histogram palette to calculate plumage hue (in degrees around a 360° color wheel), saturation, and brightness (expressed in percentages) using the color picker function (Dale, 2000).

The Arizona State University Institutional Animal Care and Use Committee approved all of the experimental procedures. Field studies were conducted under appropriate Arizona Game and Fish Department, US Fish and Wildlife Service, and US Geological Survey scientific collecting and banding permits.

Statistical analysis

Summer body mass of the four sparrow species was compared using one-way analysis of variance (1ANOVA) followed with Student-Newman-Keuls post hoc comparison tests (SNK). We compared parasite prevalence between multiple groups of sparrows using the Chi-square test for multiple independent samples when applicable (Siegel, 1956), and between two groups using the Fisher exact probability test. For each plumage feature (hue, saturation, and brightness) we analyzed differences between CASP, RWSP, and RCSP using two-way analysis of variance for repeated measures (2ANOVA) with species and the two successive measurements obtained for each bird as independent variables; these were followed with SNK tests when appropriate. Brightness data were $\log_{10}$-transformed before analysis to approach a normal distribution. Correlations between plumage features and between measurements of each feature obtained for each sparrow were determined using the Pearson product-moment correlation coefficient. The significant statistical threshold of all tests was set at $P \leq 0.05$.

RESULTS

Parasite identification

Infections with *Trypanosoma avium* were restricted to CASP, but *T. everetti* was detected in RWSP, RCSP, and BOSP. *H. fringillae* was found only in RWSP, but an unidentified *Haemoproteus* was found in a single CASP. Unidentified microfilariae were detected in all species.

Parasite prevalence during the breeding season

Prevalence of each parasite type varied among sparrow species (Table 1). The prevalence of *Haemoproteus* sp. was sig-

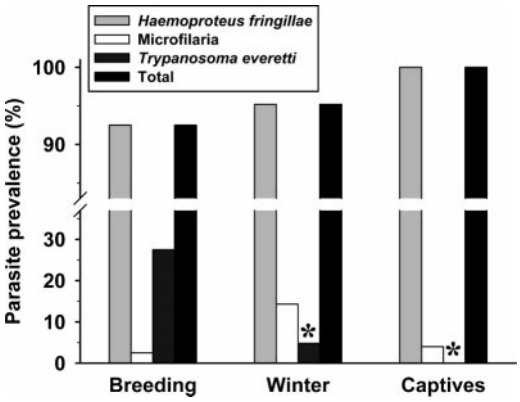

FIGURE 1. Prevalence (proportion of infected birds in a sample) of blood parasites in male rufous-winged sparrows, *Aimophila carpalis*. The figure presents data for free-ranging summer-sampled adults in breeding condition (Breeding, $n=40$), nonbreeding males (Winter, $n=21$), and adult males held in captivity and shielded from insect vectors for 1 yr (Captives, $n=25$). *Indicates a significant difference with the corresponding data for the Breeding group (Fisher exact probability test, $P \leq 0.05$).

nificantly greater ($P<0.001$) in RWSP (92.5%) than in CASP (2.5%), BOSP (0%), or RCSP (0%). The prevalence of *T. everetti* was likewise highest in RWSP, but significant differences were only detected between RWSP and BOSP ($P=0.047$). However, prevalence estimates for *Trypanosoma* sp. should be approached with some caution, because when detected, this parasite was generally found in small numbers (maximum 12 per smear in one RWSP) and in some cases may have escaped detection. The prevalence of microfilariae was significantly higher ($P=0.004$) in RCSP (30%) than in RWSP (2.5%) and CASP (2.5%).

Parasite prevalence outside the breeding season

Free-ranging RWSP ($n=21$) sampled during late fall and in winter, outside of the reproductive season (Deviche and Small, 2005), and males in breeding condition had similar prevalence of *H. fringillae* and microfilariae, but fall/winter-sampled males had a lower prevalence of *T. everetti* than summer-sampled males ($P=0.044$; Fig. 1).

TABLE 2. Hematozoan prevalence in adult male Rufous-winged Sparrows, *Aimophila carpalis*, sampled in summer 2000, 2001, and 2003 at two different sites.

		Parasite prevalence (% infected birds)		
Species	*n*	*Haemoproteus fringillae*	Microfilariae	*Trypanosoma everetti*
Site 1, 2000	13	100	15	31
Site 1, 2001	10	90	10	50
Site 2, 2003	13	92	0	38

Parasite prevalence in HY male RWSP

Prevalence of microfilariae and trypanosomes was similar in HY (microfilariae 0%; trypanosomes 18.2%) and adult RWSP, but fewer young than adults were infected with *H. fringillae* (young 63.6%; adults 92.5%; $P=0.031$). Male RWSP are, therefore, susceptible to infection with trypanosomes and *H. fringillae* within months of hatching.

Comparison of parasite prevalence between sites and years

Significant differences in prevalence for *H. fringillae*, microfilariae, or *T. everetti* were not detected between adult male RWSP caught at site 1 during 2000 and 2001 (Table 2). Differences also were not detected between prevalence estimates for these parasites from males sampled in 2000 and 2001 at site 1 compared to males sampled in 2003 at site 2. Taken together, these observations suggest that parasite prevalence in RWSP sampled during the summer in the study area was geographically uniform and did not vary between years.

Parasite prevalence in captive adult male RWSP

All males that we sampled after 1 yr of captivity were patent with *H. fringillae* (prevalence 100%; Fig. 1). Significant differences in prevalence estimates for these birds and summer-sampled free-ranging adults were detected only for *T. everetti* ($P=0.005$), which was lower in the captive birds. Thus, prolonged shielding from par-

asite vectors apparently resulted in a reduction of *T. everetti* infection or detection, but did not affect the prevalence of *H. fringillae.* Wet samples of fresh blood obtained from captive sparrows contained free *H. fringillae* gametocytes, exflagellating bodies, and gametes after 3–4 min, indicating viability of intraerythrocyte parasites.

Body mass

The average body mass of summer-sampled males varied between 15.5 g (RWSP) and 20.5 g (BOSP) and differed between species (Table 1; 1ANOVA: $F_{3,119}=154$, $P<0.001$). These masses did not overlap, that is, each species had an average body mass that differed from that of the three other species (SNK tests: $P<0.003$ for all species). Parasite prevalence did not correlate with differences in body mass.

Plumage colorfulness

The two successive measurements of each plumage characteristic (hue, saturation, brightness) taken for each bird were correlated (combined data for RCSP, RWSP, and CASP, $n=24$; BOSP not included; Pearson product-moment correlation coefficients >0.6, $P<0.002$) and did not differ (2ANOVA, $P>0.15$), indicating that these measurements were reliable and consistent. Plumage hue in RCSP, RWSP, and CASP (three species combined, $n=24$) was not correlated with plumage saturation or brightness, but saturation and brightness were negatively correlated (Pearson product-moment correlation coefficient $= -0.772$, $P<0.0001$), that is, brightest males had, on average, the least color-saturated plumage.

The degree of plumage saturation in CASP, RCSP, and RWSP differed significantly (2ANOVA: $F_{2,47}= 20.414$, $P<0.001$; Fig. 2): RCSP had a more saturated plumage than CASP, which in turn had a higher degree of saturation than RWSP (SNK tests: $P<0.05$). Plumage hue and brightness of these three species did not differ significantly (2ANOVA: hue, $P=0.09$; brightness, $P=0.071$). Data for BOSP ($n=1$) were not analyzed statistically. The plumage characteristics of the single bird of this species that was measured were closest to those of RCSP (hue, 33.0; saturation, 29.0; brightness, 62.0%; compare to data for RCSP in Fig. 2). A comparison of data in Table 1 and Figure 2 reveals that differences in plumage colorfulness were not consistently related to differences in parasite prevalence.

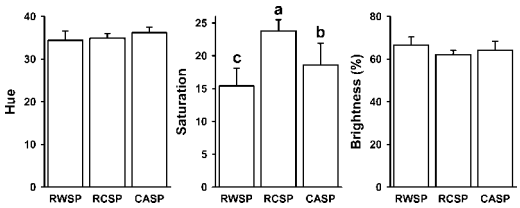

FIGURE 2. Plumage characteristics (hue, in degrees around a 360° color wheel; saturation; brightness, expressed in percentages; see text for details; $n=8$ adult males per species; means + standard deviations) of rufous-winged sparrows, *Aimophila carpalis,* rufous-crowned sparrows, *Aimophila ruficeps,* and Cassin's sparrows, *Aimophila cassinii.* Plumage saturation, but neither hue nor brightness, differed between species (*: $P\leq0.05$, Student-Newman-Keuls test).

DISCUSSION

The objectives of this study were to identify hematozoa present in Sonoran desert *Aimophila* sparrows, to compare the prevalence of these parasites among species, and to investigate mechanisms that may account for host differences in prevalence. We found sparrows to be infected with three parasite types: *Haemoproteus* sp., *Trypanosoma* sp., and microfilariae. In contrast to studies conducted on other passerines inhabiting environments other than deserts (Young et al., 1993; Norris et al., 1994; Merino et al., 1997; Rintamäki et al., 1999; Deviche et al., 2001b), no sparrow in the present study was found to be infected with *Plasmodium* or *Leucocytozoon* spp. One species (RWSP) was sampled during four different years (2000–2004) and at multiple sites, making it unlikely that absence of *Plasmodium* and *Leucocytozoon* spp. in these birds resulted

from yearly or geographical differences in infections as described for other passerines (Merilä et al., 1995; Weatherhead and Bennett, 1991). Rather, lack of detectable infection with *Plasmodium* and *Leucocytozoon* spp. in RWSP and presumably in the three other study species probably relates to factors such as absence of appropriate vectors, resistance to infection with these parasites, or ecological barriers (Laird, 1961; Blanco et al., 1998). We also found parasite prevalence to be species specific and such that the sparrows could be divided into three groups with relatively high (RWSP), intermediate (RCSP), and low (CASP, BOSP) prevalence. This classification resulted largely from differences in *H. fringillae* and to a lesser extent in microfilaria prevalence. Indeed, *Haemoproteus* prevalence exceeded 90% in RWSP, but was less than 5% in the other sparrow species, and microfilariae were detected in 30% RCSP, but in 5% or less of the birds of other species.

To address species-related variation in prevalence, we matched species in a clade that exhibit similar life histories (Introduction). In particular, we examined prevalence only in adult males of four congeneric species that were sampled in a same geographical region and during the summer, when they were in breeding condition. Within the study region, these species occupy similar and overlapping breeding habitats, and their average incubation period (11–13 days) varies by only 2 days. The present data demonstrate that observed host differences in parasite prevalence were not due to age or reproductive status. On the basis of study design, these differences apparently are also not related to duration of the incubation period, overall characteristics of breeding habitats, or differences in vector distribution or abundance.

Garvin and Remsen (1997) reported a positive relation in forest birds between plumage brightness and preferred nesting and foraging stratum. As most parasite vectors occur in mid-canopy, these authors hypothesized that Hamilton and Zuk's (1982) proposed relationship between plumage colorfulness and parasite intensity may reflect an association between nesting height and likelihood of infection, as already suggested by Bennett and Fallis (1960) and Greiner et al. (1975). If the distribution of vectors, in particular those transmitting *Haemoproteus* sp., in the Sonoran desert is stratified, as is the case in other habitats, then this hypothesis is consistent with our data. Indeed, *Haemoproteus* sp. prevalence was markedly higher in RWSP, which generally nest well above ground, than in the other *Aimophila* species, which usually nest on or close to the ground. Furthermore, most young male RWSP were infected with *H. fringillae* and some of these males also carried *T. everetti.* Thus, RWSP are susceptible to hematozoan infection during their first months of life, as is the case for other species (Bennett et al., 1982; Weatherhead and Bennett, 1992; Deviche et al., 2001a) and it is possible that infection occurs in the nest (Merino and Potti, 1995).

Parasite infection intensity and prevalence are generally higher during the reproductive period (Kucera, 1983; Weatherhead and Bennett, 1992; Deviche et al., 2001a). The prevalence of *T. everetti* observed in captive RWSP during summer, which was lower than the prevalence detected in summer-sampled free-ranging males, is consistent with a relation with reproductive period as captive birds were shielded from new infections and were kept in conditions where they could not breed. In addition, prevalence of this parasite in free-ranging males was higher in the summer reproductive period than in fall/winter, when birds were not breeding and their reproductive system was quiescent. It has been proposed that a seasonal increase in hematozoan infections results from breeding effort, which may decrease immunocompetence or induce behavioral changes favoring exposure to vectors (Norris et al., 1994; Ots and Hõrak, 1996; Allander, 1997). Our results for *T. everetti* in

RWSP are consistent with this proposition, but it is possible that the observed increase in prevalence resulted from a seasonal increase in the level of parasitemia; this would result in an increased probability of parasite detection.

In contrast to *T. everetti* prevalence, *H. fringillae* prevalence in RWSP was similar in summer field-sampled and long-term captive males. In a recent study on another passerine, *Haemoproteus belopolskyi* infection was enhanced by captivity-associated stress (Valkiünas et al., 2004). On the basis of this observation we cannot exclude the possibility that *H. fringillae* persisted in captive RWSP as a result of captivity-related stress. However, prevalence of this parasite did not differ in free-ranging adults sampled in summer and winter. In addition, 63.6% HY male RWSP were infected with this parasite during their first summer. Thus, once infected with *H. fringillae*, RWSP may express this parasite in blood chronically and perhaps indefinitely. It should be noted that this conclusion does not preclude the possibility of seasonal or age-related changes in *H. fringillae* infection intensity, and studies measuring this parameter are warranted (Fedynich et al., 1995).

Hamilton and Zuk (1982) described a positive association across passerine species between sexual displays, in particular plumage colorfulness, and parasite prevalence, and postulated that this association results from sexual selection favoring individuals with genetic resistance to disease as revealed by full expression of characters that are indicative of health and vigor. Experimental evaluation of this hypothesis has frequently been complicated by lack of clearly defined and quantitative determination of plumage showiness or colorfulness (review: Møller, 1990). To address this issue, we used the traditional tristimulus scoring method (plumage hue, saturation, and brightness) to quantify the plumage colorfulness of the four *Aimophila* species under study. Two plumage characteristics (hue, brightness) did not differ between species, but the degree of plumage saturation was highest in RCSP, intermediate in CASP, and least in RWSP. These differences did not relate to the observed differences in parasite prevalence and results do not support a relationship between hematozoan diversity or infection prevalence and plumage colorfulness.

Previous research investigated within- and between-species relationships between body mass and parasitemia. Within species, Apanius and Kirkpatrick (1988) and Merino et al. (2000) found body mass and parasitemia in female American kestrels, *Falco sparverius*, and blue tits, *Parus coeruleus*, respectively, to be negatively correlated. Such correlations may reflect a detrimental physiological impact of parasite infections (Atkinson et al., 2000; Merino et al., 2000; Yorinks and Atkinson, 2000; Dyrcz et al., 2005), but the mechanisms that mediate this impact remain uncertain as other research detected no effect of hematozoa infections on host health or viability within species (brown-headed cowbird, *Molothrus ater*, Weatherhead and Bennett, 1992). Between species, Scheuerlein and Ricklefs (2004) recently reported a positive association between body mass and prevalence of simuliid-transmitted parasites (*Leucocytozoon* sp., *Trypanosoma* sp.) in European passerines. As body surface increases with mass, this association may result from large species being more exposed to vectors and having a higher prevalence than small species. However, this association occurred at the genus and family, but not species, levels; that is, differences in body mass between congeneric species accounted for an insignificant portion of the overall (across all species considered) variation in parasitemia. Consistent with these results, we found no consistent relation between body mass and parasitemia: the body mass of the four sparrow species differed (BOSP > RCSP > CASP > RWSP), but these differences were not associated with interspecific differences in parasite prevalence. Thus, the present data offer no support to

the hypothesis of an interspecific positive relation between body surface and parasite prevalence or diversity.

ACKNOWLEDGMENTS

The authors thank Thomas Small, Joseph Georges, Russell Martin, and Matthew Ross for field assistance.

LITERATURE CITED

ADRIANO, E. A., AND N. S. CORDEIRO. 2001. Prevalence and intensity of *Haemoproteus columbae* in three species of wild doves from Brazil. Memoria Instituto Oswaldo Cruz 96: 175–178.

ALLANDER, K. 1997. Reproductive investment and parasite susceptibility in the Great Tit. Functional Ecology 11: 358–364.

APANIUS, V., AND C. E. KIRKPATRICK. 1988. Preliminary report of *Haemoproteus tinnunculi* infection in a breeding population of American kestrels (*Falco sparverius*). Journal of Wildlife Diseases 24: 150–153.

ATKINSON, C. T., R. J. DUSEK, K. L. WOODS, AND W. M. IKO. 2000. Pathogenicity of avian malaria in experimentally-infected Hawaii Amakihi. Journal of Wildlife Diseases 36: 197–204.

BARNARD, W. H., AND R. D. BAIR. 1986. Prevalence of avian hematozoa in central Vermont. Journal of Wildlife Diseases 22: 365–374.

BENNETT, G. F. 1970. Simple technique for making avian blood smears. Canadian Journal of Zoology 48: 585–586.

———, AND A. M. FALLIS. 1960. Blood parasites of birds in Algonquin Park, Canada, and a discussion of their transmission. Canadian Journal of Zoology 38: 261–273.

———, F. THOMMES, J. BLANCOU, AND M. ARTOIS. 1982. Blood parasites of some birds from the Lorraine region, France. Journal of Wildlife Diseases 18: 81–88.

BLANCO, G., A. GAJÓN, G. DOVAL, AND F. MARTINEZ. 1998. Absence of blood parasites in Griffon Vultures from Spain. Journal of Wildlife Diseases 34: 640–643.

BORTOLOTTI, G. R., J. J. NEGRO, J. L. TELLA, T. A. MARCHANT, AND D. M. BIRD. 1996. Sexual dichromatism in birds independent of diet, parasites and androgens. Proceedings of the Royal Society of London. B: Biological Sciences 263: 1171–1176.

CARDONA, C. J., A. IHEJIRIKA, AND L. MCCLELLAN. 2002. *Haemoproteus lophortyx* infection in bobwhite quail. Avian Diseases 46: 249–255.

COLLINS, P. W. 1999. Rufous-crowned parrow (*Aimophila ruficeps*). *In* The birds of North America, no. 472, A. Poole and F. Gill (eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.

DALE, J. 2000. Ornamental plumage does not signal male quality in red-billed queleas. Proceedings of the Royal Society of London. B: Biological Sciences 267: 2143–2149.

DEVICHE, P., E. C. GREINER, AND X. MANTECA. 2001a. Seasonal and age-related changes in blood parasite prevalence in dark-eyed Juncos (*Junco hyemalis,* Aves, Passeriformes). Journal of Experimental Zoology 289: 456–466.

———, ———, AND ———. 2001b. Interspecific variability of prevalence in blood parasites of adult passerine birds during the breeding season in Alaska. Journal of Wildlife Diseases 37: 28–35.

———, AND T. W. SMALL. 2005. Environmental control of reproduction in Sonoran desert *Aimophila* sparrows. Proceedings of the 8th International Symposium on Avian Endocrinology, Narosa Publishing Co., New Delhi, India. pp. 153–166.

DUNNING, J. B., JR., R. K. BOWERS, S. J. SUTER, AND C. E. BOCK. 1999. Cassin's sparrow (*Aimophila cassinii*). *In* The birds of North America, no. 471, A. Poole and F. Gill (eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.

DYRCZ, A., M. WINK, A. KRUSZEWICZ, AND B. LEISLER. 2005. Male reproductive success is correlated with blood parasite levels and body condition in the promiscuous Aquatic Warbler (*Acrocephalus paludicola*). The Auk 122: 558–565.

FEDYNICH, A. M., D. B. PENCE, AND R. D. GODFREY. 1995. Hematozoa in thin blood smears. Journal of Wildlife Diseases 31: 436–438.

GARVIN, M., AND J. V. REMSEN. 1997. An alternative hypothesis for heavier parasite loads of brightly colored birds: Exposure at the nest. The Auk 114: 179–191.

———, J. P. BASBAUM, R. M. DUCORE, AND K. E. BELL. 2003. Patterns of *Haemoproteus beckeri* parasitism in the gray catbird (*Dumatella carolinensis*) during the breeding season. Journal of Wildlife Diseases 39: 582–587.

GODFREY, R. D., D. B. PENCE, AND A. M. FEDYNICH. 1990. Effects of host and spatial factors on a haemoproteid community in Mourning Doves from Western Texas. Journal of Wildlife Diseases 26: 435–441.

GREINER, E. C, G. F. BENNETT, E. M. WHITE, AND R. F. COOMBS. 1975. Distribution of the avian haematozoa of North America. Canadian Journal of Zoology 53: 1762–1787.

HAMILTON, W. D., AND M. ZUK. 1982. Heritable true fitness and bright birds: A role for parasites? Science 218: 384–387.

KUCERA, J. 1981. Blood parasites of birds in Central Europe. 3. Plasmodium and Haemoproteus. Folia Parasitologia (Praha) 28: 303–312.

———. 1983. Incidence and some ecological aspects of avian trypanosomes in Czechoslovakia. Folia Parasitologia (Praha) 30: 209–222.

LAIRD, M. 1961. A lack of avian and mammalian haematozoa in the Antarctic and Canadian Arctic. Canadian Journal of Zoology 39: 209–213.

LINDSTRÖM, Å., AND J. O. LUNDSTRÖM. 2000. Male greenfinches (*Carduelis chloris*) with brighter or-

naments have higher virus infection clearance rate. Behavioral Ecology and Sociobiology 48: 44–51.

LOWTHER, P. E., K. D. GROSCHUPF, AND S. M. RUSSELL. 1999. Rufous-winged sparrow (*Aimophila carpalis*). *In* The birds of North America, no. 422, A. Poole and F. Gill (eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.

MCGRAW, K. J., E. A. MACKILLOP, J. DALE, AND M. E. HAUBER. 2002. Different colors reveal different information: How nutritional stress affects the expression of melanin- and structurally based ornamental plumage. Journal of Experimental Biology 205: 3747–3755.

MERILÄ, J., M. BJORKUND, AND G. F. BENNETT. 1995. Geographic and individual variation in hematozoan infections in the greenfinch, *Carduelis chloris.* Canadian Journal of Zoology 73: 1798–1804.

MERINO, S., AND J. POTTI. 1995. High prevalence of hematozoa in nestlings of a passerine species, the Pied Flycatcher (*Ficedula hypoleuca*). The Auk 112: 1041–1043.

———, J. POTTI, AND J. A. FARGALLO. 1997. Blood parasites of passerine birds from central Spain. Journal of Wildlife Diseases 33: 638–641.

———, J. MORENO, J. J. SANZ, AND E. ARRIERO. 2000. Are avian blood parasites pathogenic in the wild? A medication experiment in blue tits (*Parus caeruleus*). Proceedings of the Royal Society of London. B: Biological Sciences 267: 2507–2510.

MØLLER, A. P. 1990. Parasites and sexual selection: Current status of the Hamilton and Zuk hypothesis. Journal of Evolutionary Biology 3: 319–328.

MURATA, K. 2002. Prevalence of blood parasites in Japanese wild birds. Journal of Veterinary Medical Science 64: 785–790.

NORDLING, D., M. ANDERSSON, S. ZOHARI, AND L. GUSTAFSSON. 1998. Reproductive effort reduces specific immune response and parasite resistance. Proceedings of the Royal Society of London. B: Biological Sciences 265: 1291–1298.

NORRIS, K., M. ANWAR, AND A. F. READ. 1994. Reproductive effort influences the prevalence of haematozoan parasites in great tits. Journal of Animal Ecology 63: 601–610.

OTS, I., AND P. HÖRAK. 1996. Great Tits *Parus major* trade health for reproduction. Proceedings of the Royal Society of London. B: Biological Sciences 263: 1443–1447.

PYLE, P. 1997. Identification guide to North American birds. Part I. Columbidae to Ploceidae. Slate Creek Press, Bolinas, California, 732 pp.

RICKLEFS, R. E. 1992. Embryonic development period and the prevalence of avian blood parasites. Proceedings of the National Academy of Sciences of the United States of America 89: 4722–4725.

RINTAMÄKI, P. T., E. HUHTA, J. JOKIMÄKI, AND D. SQUIRES-PARSONS. 1999. Leucocytozoonosis and trypanosomiasis in redstarts in Finland. Journal of Wildlife Diseases 35: 603–607.

RODRIGUEZ, O. A., AND N. E. MATTA. 2001. Blood parasites in some birds from eastern plains of Colombia. Memoria Instituto Oswaldo Cruz 96: 1173–1176.

SCHEUERLEIN, A., AND R. E. RICKLEFS. 2004. Prevalence of blood parasites in European passeriform birds. Proceedings of the Royal Society of London B. Biological Sciences 271: 1363–1370.

SEUTIN, G. 1994. Plumage rednesss in redpoll finches does not reflect hemoparasitic infection. Oikos 70: 280–286.

SIEGEL, S. 1956. Nonparametric statistics for the behavioral sciences. McGraw-Hill, New York, New York, 312 pp.

TELLA, J. L., G. BLANCO, M. G. FORERO, A. GAJÓN, J. A. DONÁZAR, AND F. HIRALDO. 1999. Habitat, world geographic range, and embryonic development of hosts explain the prevalence of avian hematozoa at small spatial and phylogenetic scales. Proceedings of the National Academy of Sciences of the United States of America 96: 1785–1789.

VALKIÜNAS, G., F. BAIRLEIN, T. A. IEZHOVA, AND O. V. DOLNIK. 2004. Factors affecting the relapse of *Haemoproteus belopolskyi* infections and the parasitemia of *Trypanosoma* spp. in a naturally infected European songbird, the blackcap, *Sylvia atricapilla.* Parasitology Research 93: 218–222.

WEATHERHEAD, P. J., AND G. F. BENNETT. 1991. Ecology of red-winged blackbird parasitism by haematozoa. Canadian Journal of Zoology 69: 2352–2359.

———, AND G. F. BENNETT. 1992. Ecology of parasitism of brown-headed cowbirds by haematozoa. Canadian Journal of Zoology 70: 1–7.

———, ———, AND D. SHUTLER. 1991. Sexual selection and parasites in wood-warblers. The Auk 108: 147–152.

WEBB, E. A., AND C. E. BOCK. 1996. Botteri's sparrow (*Aimophila botterii*). *In* The birds of North America, no. 216, A. Poole and F. Gill (eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania.

YEZERINAC, S. M., AND P. J. WEATHERHEAD. 1995. Plumage coloration, differential attraction of vectors and haematozoa infections in birds. Journal of Animal Ecology 64: 528–537.

YORINKS, N., AND C. T. ATKINSON. 2000. Effects of malaria on activity budgets of experimentally infected juvenile Apapane (*Himatione sanguinea*). The Auk 117: 731–738.

YOUNG, B. E., M. C. GARVIN, AND D. B. MCDONALD. 1993. Blood parasites in birds from Monteverde, Costa Rica. Journal of Wildlife Diseases 29: 555–560.

Received for publication 2 December 2004.