Ethology

The Effect of Hemosporidian Infections on White-Crowned Sparrow Singing Behavior

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Abstract

Relatively little is known about the effects of specific parasites on sexually selected behavioral traits. We subjected free-living mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*) to a playback experiment to identify the effect of hemosporidian parasites on potentially sexually selected song characteristics. We recorded song after a playback of a novel white-crowned sparrow song, meant to simulate a territorial intrusion. Infections with *Leucocytozoon* or *Plasmodium* influenced singing behavior, while infection with *Haemoproteus* had no detectable effect. Specifically, song consistency, as measured using a spectrogram correlation, was influenced by both *Plasmodium* and *Leucocytozoon* infection. Additionally, birds infected with *Plasmodium* sang fewer songs following experimental playback. Thus, relatively widespread parasites, like *Plasmodium*, may have a strong effect on potentially sexually selected song characteristics.

Introduction

Bird song and territorial defensive behavior have intra- and inter-sexually selected functions (Andersson 1994; Catchpole & Slater 1995). For a sexually selected signal to be an honest indicator of quality, it may be costly (Zahavi 1975; Searcy & Yasukawa 1996; but see Vehrencamp 2000). Song bouts may take time away from foraging (Searcy & Yasukawa 1996), and may also increase predation risk (Gil & Gar 2002). Singing may also have some intrinsic energetic cost because it is an aerobic activity and requires potentially exhausting use of the ventilatory muscles of the body wall (Oberweger & Goller 2001), although recent studies suggest this cost is minimal (Ward et al. 2003). Males which are in some way energetically compromised may be less able to engage in singing for territorial defense and mate attraction (Ward et al. 2003). Thus, song could be a reliable indicator of male quality.

The Hamilton–Zuk hypothesis states that because male secondary sex characters require extra resources to produce and maintain, they might be differentially affected by pathogens (Hamilton & Zuk 1982). Sexually selected behaviors, like song, may be more strongly affected by parasites than morphological traits because they are relatively plastic and thus take less time to express the consequences of parasitic infection than morphological traits (Møller et al. 2000). Song traits that are sexually selected could thus serve as reliable indicators of a male's infection status to competing males as well as to prospective mates.

A number of studies have linked repertoire size, song rate and length of song bouts with male health (Møller 1991a; Buchanan et al. 1999). Females tend to prefer exaggerated song traits that can be negatively influenced by pathogens (Radesater et al. 1987; Alatalo et al. 1990). However, females probably use multiple cues to select a mate (e.g. Buchanan &

Catchpole 1997). Given the suite of advantages related to good male health, females may select these traits in part because they indicate a lack of parasitic infection and possibly the presence of genes that code for resistance (Møller 1990, 1991b).

While there is considerable evidence demonstrating that parasites may influence the expression of sexually selected traits, the relationship between bird song and parasitism is still poorly understood (but see, e.g. Saino et al. 1997; Redpath et al. 2000; Garamszegi et al. 2003, 2004). Moreover, few previous studies have focused on the individual effects of specific parasites. In fact, such singular focus has been criticized on the grounds that it might obscure evidence of parasite-mediated sexual selection because any given vertebrate may be host to many species of parasites, and the influence of any one parasite on host fitness is likely to be small (Møller et al. 2000). In reality, each species of parasite, even within a relatively circumscribed group, such as the hemosporidians, has a different life cycle, frequently utilizing different host tissues. As a result, infection with each parasite is characterized by a different set of symptoms, and ultimately produces different levels of overall virulence (Atkinson & van Riper 1991). For example, because *Plasmodium*, the causal agent of avian malaria, undergoes erythrocytic schizogony and regularly produces anemia in its hosts (Valkiunas 2005), aerobically demanding functions may be particularly impaired among infected hosts. Overall, given their differing impacts on the host, some parasites may have a more negative influence on sexually selected characters, and thus be more important in parasite-mediated sexual selection.

In this study, we focus on the effects of hemosporidians (a group of protozoan parasites) on the song of mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*). The most important hemosporidians parasitizing birds belong to the genera, *Leucocytozoon*, *Haemoproteus* and *Plasmodium*. These parasites have been studied extensively and provide a good 'reference system' for observing the influence of parasites on sexually selected characters (Atkinson & van Riper 1991; Burry-Caines & Bennett 1992; Bennett et al. 1994; Valkiunas 2005). Although much of our understanding of the detrimental effects of these parasites on avian hosts comes from the atypical host–parasite interactions on the Hawaiian islands (Warner 1968; van Riper et al. 1986; Jenkins et al. 1989; Atkinson et al. 1995, 2000, 2001), an increasing body of literature has examined these host–parasite interactions in more typical mainland ecosystems (e.g. Boyce 1990; MacDougall-Shackleton et al. 2002; Korpimäki et al. 1993; Valkiunas 2005). Traditionally, such parasites were considered to be relatively non-pathogenic in wild birds (Bennett et al. 1993), but it is now clear that they can have profound effects on the reproduction (Korpimäki et al. 1993), physiology (Atkinson et al. 2001), behavior (MacDougall-Shackleton et al. 2002; Valkiunas 2005) and ecology of their hosts (Derryberry et al. 2003), as well as on the dynamics and persistence of host populations (van Riper et al. 1986). Given their potential impacts on the lifetime reproductive success of the host and the importance of a host's overall genetic health in controlling parasitemias (MacDougall-Shackleton et al. 2005), it is reasonable to expect song to reflect not only on a male's general infection status, but also to provide information on infection with particular parasites.

If the Hamilton–Zuk hypothesis is broadly applicable, infected male white-crowned sparrows should sing impaired songs, perhaps by singing less often, singing at slower rates, or producing inconsistent and more variable songs. Alternatively, other factors, such as overall body condition or age, may play a larger part in song quality, as well as degree of arousal. In either case, differences between males should become more pronounced when a male is challenged by a foreign male intruder.

Methods

Study Sites

We trapped, measured and recorded sparrows in four previously established sites (J. Foufopoulos, unpublished data) in mountain white-crowned sparrow habitat along the East River Valley, north of Rocky Mountain Biological Laboratory, Gothic, CO (38°95′N, 106°98′W, 3150 m). The vegetation on the study plots consists of a patchwork of alpine meadows and willow thickets in which the sparrows breed. The sites measured approximately 200 m by 400 m, were 200–300 m apart and, in 2003, contained a total of 68 distinct known sparrow territories. While there was acoustic variation within and across our study plots, the population as a whole could be said to sing one dialect.

Trapping and Drug Administration

We used millet-baited potter traps and mist-nets to capture the birds on a regular schedule, between 06:00–12:00 hours, throughout the months of Jun. and Jul. 2003. During this period, we captured 51 males and the number of captures for each male varied substantially (x = 3.45, range 1–12). After each capture, we collected a blood sample (no more than 300 μl in a 2-week period) from a small puncture in the brachial vein using micro-capillary tubes and, to obtain indicators of condition, we measured each male's mass and tarsus length. Two blood smears were prepared from each sample using standard microscope slides, air dried and stained with a Fisher Hema 3 Stat pack^{TM} (Fisher Diagnostics, Middletown, VA, USA). We determined the infection status of each bird based on the evaluation of the blood smear collected closest to the time of the recording. We searched each slide systematically for parasites for 20 min using a compound microscope at 1000× magnification, therefore ensuring equal detection effort for all samples. During this period, we examined a minimum of 10 000 red blood cells; based on previous experience, this effort is sufficient to detect the vast majority of hemoparasite infections.

All mountain white-crowned sparrows captured on the study plots since 1999 have been marked upon first capture with a metal US Fish and Wildlife Service band (Bird Banding Laboratory, Patuxent, MD, USA) and a unique combination of three plastic color bands for visual identification in the field. Based on the date when each bird was first banded, we calculated the minimum age of each individual.

To ensure a random sample of uninfected birds, we administered an antiprotozoal agent to half of our study population. Birds with odd-numbered bands (22/51) received the drug treatment, while control birds (29/51) received equal volume of placebo (water). Birds received their respective treatment each time they were captured and were handled in the same manner independent of treatment group assignment. The agent was an aqueous solution of sulfadimethoxine (50 mg/kg) and pyrimethamine (1 mg/kg), a mix that has been shown to suppress protozoal infections in birds (Valentin et al. 1994; Huchzemeyer 1996; Fukui et al. 2002). This drug cocktail was administered orally using a graduated syringe with the needle removed. Based on our field observations, the agent has no discernable effects on behavior and was shown to be effective in suppressing hemosporidian infections in our subjects: birds that received multiple doses tended to be free of the focal blood parasites (Fisher's exact test $p = 0.003$, $n = 45$). However, because the agent was not 100% effective, we relied on smear data, rather than treatment status, to determine parasite infection status for each individual. Hence, the purpose of this drug administration was not to detect any treatment effects per se, but to partially randomize the presence of hemoparasites in the population.

Playback Procedure and Recordings

Between 06:00 and 12:00 hours, we subjected only males actively engaged in song to a playback experiment to standardize the sampling method, ensure a response and ensure the male was within its territory. Once a male singing in its own territory was identified, one of us (SG) approached at a slow deliberate pace and placed a speaker on the ground 7–10 m from its perch. The researcher (SG) then retreated back an additional 5–10 m, depending on the available cover, to avoid alarming the bird.

If the approach was successful (i.e. we did not displace the bird), we simulated an act of aggression on its territory by playing 2 min (four songs per min) of song recorded from one of two different males that lived in a different region of the valley (Fig. 1).

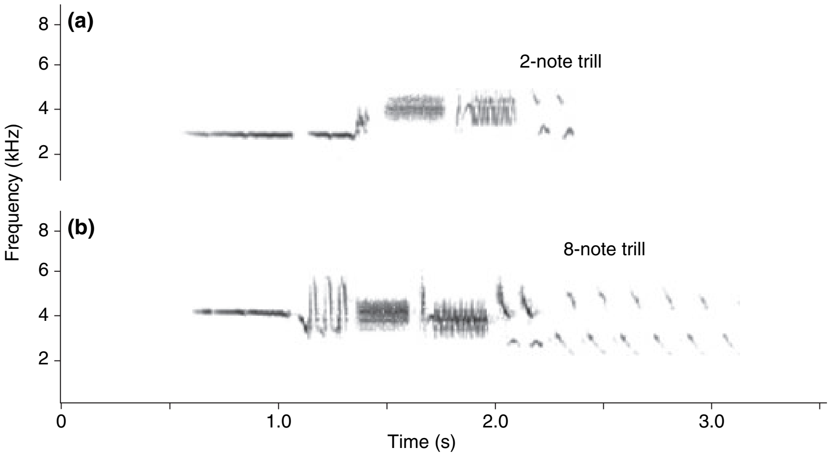

Fig. 1: Spectrograms of songs from two different adult male white crowned sparrows recorded in the East River Valley, near Gothic, CO, illustrating the variation in song structure. (a) Illustrates a song with a two-note trill. (b) Illustrates a song with an eight-note trill

When the focal subject resumed singing, we recorded its song for 2 min and noted the number of perches it sang from assuming that birds that sang from more perches were more responsive. Song was recorded from an average of 12.3 m (± 6.5 SD) with a Sennheiser MH 816 directional microphone (Sennheiser, Wennebostel, Germany) and a Sony TC-D5M cassette recorder (Sony Corporation, Tokyo, Japan) onto hi-bias cassette tapes during the period after territory establishment and before the end of the breeding season (10 Jun. to 18 Jul. 2003). We collected usable recordings from 34 of the 68 known males in the study sites. Songs were recorded on an average 7 (±1.98 SE) days from the most recent blood smear.

Song Analysis

White-crowned sparrows sing in a variety of geographically segregated song dialects (Orejuela & Morton 1975; Cunningham et al. 1987). *Zonotrichia leucophrys oriantha* songs range 2–7 kHz and last 2–3 s (Chilton et al. 1995). The initial component of the song contains several 'pure tone' whistles followed by a complex sequence of buzzy elements and finally a trill of variable length containing between two and eight notes (Chilton et al. 1995, Fig. 1).

If birds sang at ≥4 songs per min, we digitized at least eight songs from the 2-min recording using Canary 1.2.4 (Cornell Laboratory of Ornithology, Ithaca, New York, USA) (Charif et al. 1998). If birds sang <4 songs per min, we digitized all recorded songs. Songs were digitized at 16 bit, 44.1 kHz resolution and band-pass filtered at 2.5–7.0 kHz to minimize background noise. We then generated spectrograms (Fig. 1) for all songs (analysis resolution: filter bandwidth = 349.70 Hz, frame length = 512 points; grid resolution: time = 2.902 ms, overlap = 75%, frequency = 43.07 Hz, FFT size = 1024 points; window function: Hamming, clipping level = −80 dB).

As male mountain white-crowned sparrows stabilize at a single song type in their first breeding season and use the same song in subsequent seasons (Chilton et al. 1995; Nelson 2000), song quality might be indicated by inter-song consistency rather than repertoire size as with birds which vary their song (e.g. Hasselquist et al. 1996; Ballentine et al. 2003). We calculated inter-song variation in two ways.

We used Canary to generate all possible pair wise, peak-normalized spectrogram cross-correlations (Clark et al. 1987) to compare songs randomly sampled (n = 5–10) from the 2-min period of recording following the simulated aggression. We calculated the mean and coefficient of variation of the values in the matrix below the diagonal, and used these as overall measures of song consistency for each bird. We counted the number of notes per trill from spectrograms, and calculated the mean and coefficient of variation for each bird.

Song rate might also be a measure of quality (Alatalo et al. 1990). Rate after playback was determined by counting the number of songs in the 2-min period after the bird resumed singing rather than the 2 min time window directly following the playback.

Statistical Analyses

We fitted a MANCOVA model to the data to identify the effect of each parasite on song structure and response after controlling for variation explained by age and condition (estimated from residuals of mass regressed against tarsus). Dependent variables included the mean number of trill notes/song, the coefficient of variation of the number of trill notes/song, the number of songs every 2 min, the spectrogram correlation mean, and the number of perches sung from. Independent variables included age, condition and the infection status for each of the three parasites. We also calculated the marginal mean values to aid in interpretation of the effects of specific parasites on significant song traits, and we calculated partial eta-square as a measure of a parameter's effect size. All residuals from these models either appeared normal or approximated a normal distribution; transformations were not required to normalize data. We used SPSS 11.5 to analyze all data and interpret values of $p < 0.05$ as statistically significant.

Results

Overall, 22 of the 34 birds (65%) in the recorded sample were infected with at least one of the three focal pathogens. Of these, 17 birds were infected with *Leucocytozoon* (50%), nine were infected with *Haemoproteus* (26%) and seven were infected with *Plasmodium* (21%). Cross-infection frequencies are given in Table 1.

The MANCOVA model revealed large and significant effects of *Leucocytozoon* and *Plasmodium* infections on measured song characteristics (Table 2). While there were no other significant main effects, the effect sizes of condition and age were moderate (Table 2).

An analysis of the constituent models showed that only the spectrogram correlation means ($p < 0.001$), and the number of perches sung from ($p = 0.015$) were significantly influenced by infection status (Table 3). *Leucocytozoon* infection significantly

Table 1: Cross-infection status of infected white-crowned sparrows (i.e. five birds were infected with *Leucocytozoon* and *Haemoproteus*, six with *Leucocytozoon* and *Plasmodium*, etc.)

	Leucocytozoon	*Haemoproteus*	*Plasmodium*
Leucocytozoon	6	5	6
Haemoproteus		4	0
Plasmodium			1

Numbers on the diagonal represent birds with single type of infection. Birds infected with *Leucocytozoon* were likely to be infected with *Haemoproteus* and *Plasmodium*, birds infected with *Haemoproteus* were likely to be infected with only *Leucocytozoon*, and birds infected with *Plasmodium* were likely to be infected with *Leucocytozoon*.

($p < 0.001$) increased spectrogram correlation mean values by 36.2%, while *Plasmodium* infection significantly ($p < 0.001$) decreased spectrogram correlation mean values by 55.3% (Fig. 2). Additionally, *Plasmodium* infection significantly ($p = 0.001$) reduced the number of songs sung post-playback by 43.5% (Fig. 2).

Discussion

Infection with certain hemoparasites significantly influenced singing behavior in male mountain white-crowned sparrows. While the pattern of cross-infection made it difficult to identify specific effects, infection with *Plasmodium* reduces both song output and song consistency. Infection with *Leucocytozoon*, on the other hand, also influences song structure by increasing song consistency without any obvious effects on any of the other song characteristics. While it is clear that additional formal experimental manipulations are warranted, these results suggest that both song variability and song output should be examined in future studies.

The diversity of effects of hemoparasitism on song may be explained by the different pathologies of infection caused by each hemosporidian taxon. For example, infections with *Leucocytozoon* resulted in decreased song variability as quantitated through spectrogram correlation means. Although many *Leucocytozoon* infections do not appear to result in increased adult mortality (Atkinson & van Riper 1991), several published reports exist on adult morbidity and mortality (see Valkiunas 2005 and references therein). *Leucocytozoon* species are also known to produce severe epidemics especially in Anatids and Galliformes (Valkiunas 2005). Many *Leucocytozoon* taxa form massive accumulations of meronts (magalomeronts) in fixed tissues, such as the spleen, liver, lungs, etc. When these clusters form in the brain, they can result in severe central nervous system pathologies including cerebral hemorrhage, paralysis or death (Valkiunas 2005). It is hence possible that milder brain infiltrations of this type and the accompanying host inflammatory response are responsible for the changes in song variability observed in this study. In contrast to *Plasmodium*, *Leucocytozoon* does not regularly impact aerobic capacity. In line with this observation, we found that infection with *Leucocytozoon* did not impair the ability of a bird to move around and broadcast a large number of songs from multiple perches in its territory.

Our analysis points to a statistically significant interaction between *Leucocytozoon* and *Plasmodium* infections on the ability of birds to produce consistent songs. Because both of these parasite genera can impact brain function, although in different ways, it is possible that dual infections have more than additive effects on host song.

The proportion of birds infected with *Plasmodium* was smaller than the proportion of birds infected with either of the other focal parasites. *Plasmodium* is considered to be more virulent than other hemosporidians that afflict birds (van Riper et al. 1986; Atkinson & van Riper 1991; Valkiunas 2005). For example, an important symptom of *Plasmodium*

Table 2: Overall MANCOVA results illustrating the effects of hemosporidian infections, after controlling for the effects of condition and age, on singing behavior in male white-crowned sparrows

Effect	Value (Roy's largest root)	p-value	Partial eta squared
Intercept	17.841	**<0.001**	0.947
Condition	0.992	0.101	0.498
Age	0.513	0.353	0.339
Leucocytozoon	2.913	**0.003**	0.774
Haemoproteus	0.174	0.828	0.148
Plasmodium	6.635	**<0.001**	0.869
Leucocytozoon × *Haemoproteus*	0.598	0.281	0.374
Leucocytozoon × *Plasmodium*	7.095	**<0.001**	0.876
Haemoproteus × *Plasmodium*	<0.001	1.000	**<0.001**
Leucocytozoon × *Haemoproteus* × *Plasmodium*	<0.001	1.000	**<0.001**

Significant p-values are highlighted in bold.

Table 3: MANOVA results illustrating the effects of hemosporidian infections, after controlling for the effects of condition and age, on specific aspects of singing behavior in male white-crowned sparrows

	Dependent variable	p-value	Partial eta squared
Model	Mean no. of trill notes/song	0.301	0.367
	CV of the no. of trill notes/song	0.284	0.374
	Spectrogram correlation mean	**<0.001**	0.875
	No. of songs/2 min	**0.015**	0.614
	No. of perches sung from	0.143	0.449
Intercept	Mean no. of trill notes/song	**0.001**	0.478
	CV of the no. of trill notes/song	0.394	0.046
	Spectrogram correlation mean	**<0.001**	0.922
	No. of songs/2 min	**0.001**	0.502
	No. of perches sung from	**0.009**	0.355
Condition	Mean no. of trill notes/song	0.306	0.065
	CV of the no. of trill notes/song	0.200	0.101
	Spectrogram correlation mean	0.139	0.132
	No. of songs/2 min	0.593	0.018
	No. of perches sung from	0.054	0.213
Age	Mean no. of trill notes/song	0.958	<0.001
	CV of the no. of trill notes/song	0.685	0.011
	Spectrogram correlation mean	0.289	0.070
	No. of songs/2 min	0.092	0.167
	No. of perches sung from	0.574	0.020
Leucocytozoon	Mean no. of trill notes/song	0.852	0.002
	CV of the no. of trill notes/song	0.969	<0.001
	Spectrogram correlation mean	**<0.001**	0.628
	No. of songs/2 min	0.071	0.190
	No. of perches sung from	0.631	0.015
Haemoproteus	Mean no. of trill notes/song	0.266	0.077
	CV of the no. of trill notes/song	0.405	0.044
	Spectrogram correlation mean	0.849	0.002
	No. of songs/2 min	0.351	0.054
	No. of perches sung from	0.535	0.024
Plasmodium	Mean no. of trill notes/song	0.158	0.120
	CV of the no. of trill notes/song	0.842	0.003
	Spectrogram correlation mean	**<0.001**	0.744
	No. of songs/2 min	**0.001**	0.501
	No. of perches sung from	0.096	0.163
Leucocytozoon × *Haemoproteus*	Mean no. of trill notes/song	0.086	0.173
	CV of the no. of trill notes/song	0.450	0.036
	Spectrogram correlation mean	0.710	0.009
	No. of songs/2 min	0.454	0.035
	No. of perches sung from	0.439	0.038
Leucocytozoon × *Plasmodium*	Mean no. of trill notes/song	0.585	0.019
	CV of the no. of trill notes/song	0.131	0.136
	Spectrogram correlation mean	**<0.001**	0.798
	No. of songs/2 min	0.131	0.136
	No. of perches sung from	0.417	0.042
Haemoproteus × *Plasmodium*	Mean no. of trill notes/song	–	<0.001
	CV of the no. of trill notes/song	–	<0.001
	Spectrogram correlation mean	–	<0.001
	No. of songs/2 min	–	<0.001
	No. of perches sung from	–	<0.001
Leucocytozoon × *Haemoproteus* × *Plasmodium*	Mean no. of trill notes/song	–	<0.001
	CV of the no. of trill notes/song	–	<0.001
	Spectrogram correlation mean	–	<0.001
	No. of songs/2 min	–	<0.001
	No. of perches sung from	–	<0.001

Significant effects are highlighted in bold.

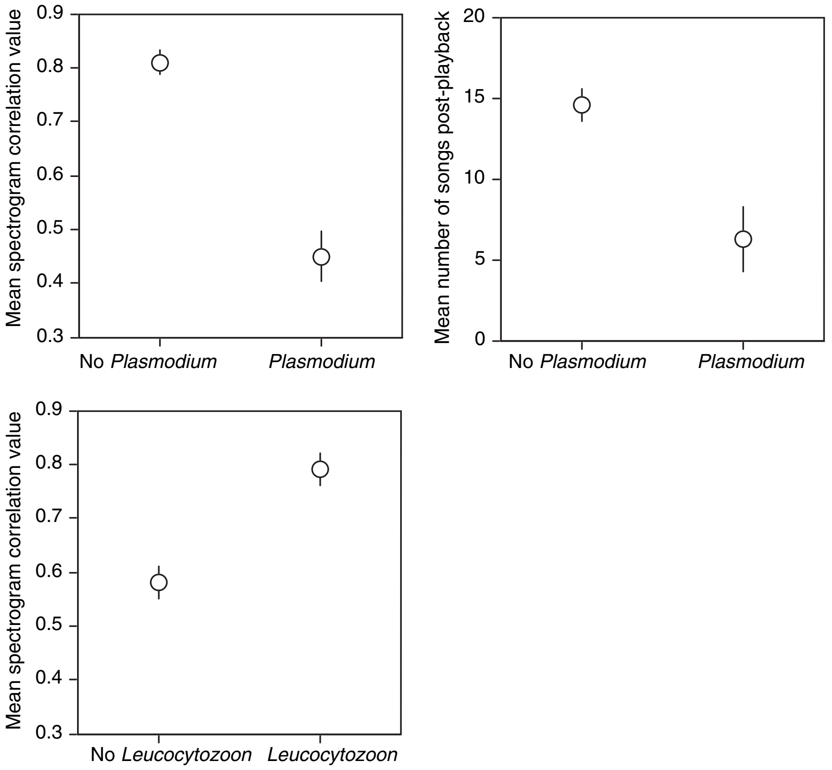

Fig. 2: Marginal mean (± SE) spectrogram correlation values and/or number of songs sung post playback as a function of infection status

infections may also be responsible for some of the observed patterns: because parasites colonize the lining of brain capillaries, they can impede or even block blood flow to functionally important brain regions. In severe cases, this may cause neurological symptoms (Karstad 1965; Stone et al. 1971; Atkinson & van Riper 1991), but it is possible that milder infections may impact the ability of an infected male brain to produce an acoustically consistent song. More importantly, the destruction of blood cells by protozoan hemoparasites as well as an excessive immune response can result in host anemia (Atkinson & van Riper 1991). The concomitant decrease in aerobic function may impair a bird's ability to produce a large number of songs as observed during our experimental intrusions.

Our results suggest that each type of infection produces a distinct fingerprint on song rate and structure. It has been proposed that different parasites affect different sexual characters (Wedekind 1992). This proposal makes the most sense for disparate characters like song and plumage. However, as different aspects of song may be influenced by different mechanisms (Garamszegi 2005), this could also apply to the differences produced by the various parasites in this study. Our analysis points to a statistically significant interaction between *Leucocytozoon* and *Plasmodium* infections on the ability of birds to produce consistent songs. Because both of these parasite genera can impact brain function through different pathways, it is possible that dual infections have more than additive effects on host song. In any case, given the apparent complexity of infection effects on mountain white-crowned sparrow song, it is conceivable that male aggressors and potential mates are able to obtain information not only on whether a male is infected, but also what type of hemoparasite it carries.

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