

PREVALENCE OF BLOOD PARASITES IN MIGRATING AND WINTERING CALIFORNIA HAWKS

HEATHER D. ISHAK¹ AND CLAIRE LOISEAU

Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132 U.S.A.

ANGUS C. HULL

Golden Gate Raptor Observatory, Building 1064, Fort Cronkhite, Sausalito, CA 94965 U.S.A.

RAVINDER N.M. SEHGAL²

Department of Biology, San Francisco State University, 1600 Holloway Avenue, San Francisco, CA 94132 U.S.A.

ABSTRACT.—Infectious diseases can potentially affect the seasonal migration of hawks. We tested three species of California hawks from autumn 2004 to spring 2006 for haemosporidian blood parasites (*Plasmodium*, *Haemoproteus*, and *Leucocytozoon* spp.). We screened 323 Red-tailed Hawks (*Buteo jamaicensis*), 100 Cooper's Hawks (*Accipiter cooperii*), and 21 Red-shouldered Hawks (*B. lineatus*) for blood parasites using polymerase chain reaction (PCR). Among these hawks, 221 (50%) were infected with *Haemoproteus*, 134 (30%) with *Leucocytozoon*, and none with *Plasmodium* species. We compared blood parasite prevalence results to identify infection patterns in two populations (birds captured during autumn at a migration watchsite in the Marin Headlands [Golden Gate Raptor Observatory] vs. birds captured during winter in the Central Valley) and between years, seasonal periods, and sex and age classes. In 2004, Marin Red-tailed Hawks were more likely to test positive for blood parasites if sampled late in the migration; however, we observed the opposite pattern in Cooper's Hawks. The prevalence of both *Haemoproteus* and *Leucocytozoon* followed the same seasonal trends in each host species, which suggested a possible effect of infection status on raptor migration. We also observed different patterns of variation in parasite prevalence between years at the two sampling sites, but no significant differences between juvenile and adult birds at either site. In addition, using a simple measure of body condition, we observed significant differences between males and females with regard to the effects of parasite infection and sampling location. These results provide a baseline for future studies monitoring long-term changes in parasite prevalence and effects on California's migrating hawks.

KEY WORDS: *Cooper's Hawk*; *Accipiter cooperii*; *Red-tailed Hawk*; *Buteo jamaicensis*; *blood parasites*; *migration*.

PREVALENCIA DE PARÁSITOS SANGUÍNEOS EN RAPACES MIGRANTES E INVERNANTES EN CALIFORNIA

RESUMEN.—Las enfermedades infecciosas tienen el potencial de afectar la migración estacional de las aves de presa. Hicimos pruebas para detectar la presencia de parásitos sanguíneos hemosporidios (*Plasmodium*, *Haemoproteus* y *Leucocytozoon* spp.) en tres especies de California. Hicimos pruebas basadas en la reacción en cadena de la polimerasa (PCR) para detectar parásitos sanguíneos en 323 individuos de la especie *Buteo jamaicensis*, en 100 de *Accipiter cooperii* y en 21 de *B. lineatus*. De estos individuos, 221 (50%) estaban infectados con *Haemoproteus*, 134 (30%) con *Leucocytozoon* y ninguno con *Plasmodium*. Comparamos los resultados de prevalencia de parásitos sanguíneos para identificar los patrones de infección en dos poblaciones (individuos capturados durante el otoño en un sitio de observación de la migración en los promontorios de Marin [Golden Gate Raptor Observatory] vs. aves capturadas durante el invierno en el valle Central) y entre años, estaciones y clases de sexo y edad. En 2004, los individuos de *B. jamaicensis* de Marin presentaron una mayor probabilidad de mostrar resultados positivos sobre la presencia de parásitos sanguíneos si fueron examinados más tarde durante la migración. Sin embargo, observamos el patrón opuesto en *A. cooperii*. La prevalencia de *Haemoproteus* y de *Leucocytozoon* mostró las mismas tendencias estacionales

¹ Present address: Section of Integrative Biology, University of Texas, Austin, TX 78712 U.S.A.

² Email address: sehgal@sfsu.edu

en cada especie de hospedero, lo que sugirió un posible efecto del estado de infección sobre la migración de las rapaces. También observamos patrones diferentes de variación en la prevalencia de parásitos entre años en los dos sitios de muestro, pero no detectamos diferencias significativas entre aves jóvenes y adultas en ningún sitio. Además, empleando una medida simple de la condición corporal, observamos diferencias significativas entre machos y hembras con respecto a los efectos de la infección con parásitos y del sitio de muestro. Estos resultados brindan una base para estudios futuros de monitoreo de los cambios de largo plazo en la prevalencia de parásitos y sus efectos sobre las rapaces migratorias de California.

[Traducción del equipo editorial]

Blood parasites are commonly found in birds and can have serious consequences for their hosts during energy-demanding periods such as migration and reproduction (Remple 2004, Garvin et al. 2006). Migratory birds often have higher prevalences of blood parasites than nonmigrants (Møller and Erritzøe 1998). This has been attributed to the stress of migration and the fact that migrants move through more terrain, which increases the likelihood of encountering a higher diversity of parasite vectors (Møller and Erritzøe 1998, Smith et al. 2004, Valkiūnas 2005). Although migration occurs in both spring and autumn, most previous parasite studies have focused on spring migration due to the increased prevalence of haematozoan infections in spring and summer (Allander and Bennett 1995, Phalen et al. 1995, Rintamäki et al. 1998, 1999, Dawson and Bortolotti 2000, Dyrce et al. 2005, Garvin et al. 2006). Few studies have examined blood parasites during autumn and winter months when parasite infections likely become latent (Schrader et al. 2003, Garvin et al. 2004, Smith et al. 2004).

Migration requires a significant energy investment and is an especially treacherous time for juvenile birds (Clarabuch and González-Solís 1998). Hawks, in particular, have high first-year mortality rates. Band recovery data suggest that first-year mortality rates can range from 50–83% (Newton 1979). Although most blood parasites are thought to be nonpathogenic, parasite-induced fatalities can occur within a bird's first year of life (Davidar and Morton 1993, Leppert et al. 2004). Parasite infections acquired by nestlings presumably could negatively affect both the timing of migration departure and the bird's ability to survive (Hunter et al. 1997, Leppert et al. 2004). Thus, blood-parasite studies during autumn and winter may reveal parasite effects on migrating juvenile hawks.

We studied blood-parasite prevalences in three hawk species (Accipitridae) sampled in California. We examined Red-tailed Hawks (*Buteo jamaicensis*), Red-shouldered Hawks (*B. lineatus*), and Cooper's Hawks (*Accipiter cooperii*) captured at an autumn mi-

gration count site in the Marin Headlands on the central coast, and wintering Red-tailed Hawks and Red-shouldered Hawks captured in the Central Valley. Taking seasonality into consideration, we examined differences in blood parasite prevalence between the two study populations and between sex and age classes.

METHODS

Sample Collection. We collected blood samples from hawks captured during autumn at the Golden Gate Raptor Observatory (GGRO) migration watch-site located in the Marin Headlands, Sausalito, CA (37°40'N, 122°20'W) and from a dense concentration of wintering hawks in the northern Central Valley of California (38°05'–39°57'N, 121°22'–122°17'W). We captured hawks at the GGRO site between 15 August and 19 December in 2004 and 2005 using bow nets, dho-gaza traps, and mist nets (Bloom et al. 2007). We captured wintering raptors using bal-chatri traps along roadsides (Berger and Mueller 1959) from 26 November 2004 to 6 March 2005 and from 25 November 2005 to 22 February 2006. In this study, the 2004 season refers to all birds captured from August 2004 through March 2005, and the 2005 season encompasses all captures from August 2005 through February 2006.

We banded each captured hawk with a U.S. Geological Survey aluminum leg band, identified each to species and approximate age, and measured mass and wing chord for each. We determined the sex of Red-tailed Hawks as described by Pitzer et al. (2008). We also collected a few drops of blood from the medial metatarsal vein of each bird. We used one drop of blood to make a blood smear fixed with methanol and stained with Giemsa (Godfrey et al. 1987). We placed the rest of the blood sample in 1 ml of lysis buffer (Sehgal et al. 2006) and stored it in a –20°C freezer. All captured hawks appeared healthy and were released at the trap site.

Parasite Detection. We extracted parasite DNA and screened blood samples for *Leucocytozoon* spp. following methods described by Sehgal et al. (2006).

To test for *Plasmodium* and *Haemoproteus* spp., we used a second PCR protocol that amplifies the cytochrome *b* region of the mtDNA. For this PCR reaction we used the same PCR components from Sehgal et al. (2006) with the following primers: L15183 and H15730 (Fallon et al. 2003, Szymanski and Lovette 2005). This PCR reaction does not distinguish between the two parasite genera. The cycling profile is similar to Sehgal et al. (2006) with a denaturing step for 50 sec and an annealing temperature of 53°C for 50 sec.

We used positive and negative controls to detect *Plasmodium*, *Haemoproteus*, and *Leucocytozoon*. Positive controls were from birds with known infections evident from microscopy results, and we used water for the negative controls. We visualized the PCR products on 2% agarose gels stained with ethidium bromide under UV light.

To distinguish between the *Plasmodium* and *Haemoproteus* genera, we sequenced DNA from 88 hawks (64 Red-tailed Hawks and 24 Cooper's Hawks) using the L15183 and H15730 primers. We performed bidirectional sequencing with dye-terminator fluorescent labeling in an ABI Prism 3100 automated sequencer (Applied Biosystems, Inc., Foster City, California, U.S.A.). We sequenced 512 base pairs and edited them using Sequencher 3.1 (GeneCodes, Ann Arbor, Michigan, U.S.A.). We then identified sequences to genus by identifying their closest sequence matches in GenBank via the National Center for Biotechnology Information (NCBI) nucleotide BLAST search. The most similar sequences were all *Haemoproteus* spp. with the following accession numbers: AF465592, AF46591, and AF465593.

We conducted phylogenetic analyses using maximum parsimony techniques and PAUP* 4.0b10 (Swofford 2002). Searches used the bootstrap search option with 1000 stepwise addition replicates and the TBR branch-swapping algorithm. We constructed a simple consensus tree to summarize the results and estimated genetic divergences using the HKY85 setting. We deposited all sequences in GenBank (FJ966919 to FJ966927).

We examined some Giemsa-stained slides for haemsporidian parasites using a Nikon E200 compound microscope at 100×, 400×, and 1000×.

Statistical Tests. We first used a one-way chi-square test to evaluate overall differences among species in prevalences of the two parasite genera (*Haemoproteus* sp. and *Leucocytozoon* sp.). We then used multiple logistic regression to determine if there were significant differences within host spe-

cies in the prevalence (binary response variable: infected or not) of different blood parasites (*Haemoproteus* and *Leucocytozoon* analyzed separately) between years (2004 vs. 2005), age groups (juvenile vs. adult), regions (Marin Headlands vs. Central Valley) and date of capture (before and after 15 October). We ran these models for Red-tailed Hawks and Cooper's Hawks, but not for Red-shouldered Hawks due to small sample sizes. The Red-tailed Hawk model included all variables plus all relevant two- and three-way interactions, whereas the Cooper's Hawk model included only year, age, and date of capture, because we sampled this species only in the Marin Headlands. We tested the association between infection status and predictor variables using generalized linear models (Proc GENMOD with binomial distribution of errors and logit link function; SAS Institute 1999).

We also investigated relationships between body condition and the occurrence of blood parasites. We considered only Red-tailed Hawks for these analyses due to small sample sizes and incomplete sets of mass and wing-length data for Cooper's Hawks and Red-shouldered Hawks. We calculated an index of body condition as measured by residuals from an ordinary least squares (OLS) regression of mass against a flat wing measurement (Schulte-Hostedde et al. 2005). Red-tailed Hawks exhibit sexual dimorphism, wherein females tend to be heavier than males, although substantial overlap exists (Pitzer et al. 2008). To account for the effect of sex on our body condition indices, we calculated the OLS residuals individually for each sex. We then ran an ANOVA to test for relationships between body-condition indices and explanatory variables: one infection-status variable for each parasite (binary: yes or no), sex (male vs. female), year (2004 vs. 2005), age (juvenile vs. adult), region (Marin Headlands vs. Central Valley), date of capture (before and after 15 October), and relevant two-way interactions.

RESULTS

We collected blood samples from 323 Red-tailed Hawks (Marin Headlands: $n = 183$; Central Valley: $n = 140$), 100 Cooper's Hawks (Marin Headlands: $n = 100$), and 21 Red-shouldered Hawks (Marin Headlands: $n = 6$; Central Valley: $n = 15$). Among these, 134 of 446 (30%) tested positive for *Leucocytozoon* and 221 (49.5%) tested positive for *Haemoproteus/Plasmodium* infections. Sequencing of parasite mtDNA from a subset of hawks ($n = 88$) revealed eight lineages of *Haemoproteus* infections, but no cas-

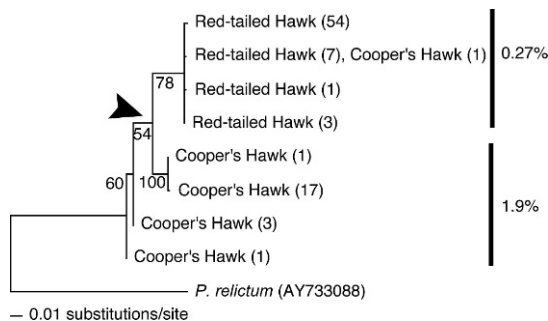


Figure 1. Maximum likelihood phylogram of *Haemoproteus* spp. parasites in Red-tailed Hawks and Cooper's Hawks. The maximum likelihood bootstrap values (100 replicates) are placed below branches. The number of individuals sequenced for each species is in parentheses. Sequence divergence between the Red-tailed Hawk and Cooper's Hawk groups (4.0%) is indicated by an arrow at the major branch point. Intraspecific sequence divergence is indicated by black bars to the right of the classification tree. *Plasmodium relictum* (with its Genbank identifier in parentheses) was used as an outgroup.

es of *Plasmodium* infection. In Red-tailed Hawks, the species visible was *Haemoproteus elani*, but blood smears were of insufficient quality to identify species in Cooper's Hawks (G. Valkiūnas unpubl. data). Maximum likelihood and HKY85 distance analyses identified two *Haemoproteus* clades with a 4% average

sequence divergence (Fig. 1). One clade was specific to Cooper's Hawk parasites with intraspecific variation of 1.9%, and a second clade consisted of mostly Red-tailed Hawk parasites with intraspecific sequence divergence of 0.3%.

Overall blood-parasite prevalence was highest in Cooper's Hawks (61.2% *Leucocytozoon*, 49.8% *Haemoproteus*) and lowest in Red-shouldered Hawks (9.5% *Leucocytozoon*, 14.3% *Haemoproteus*; Table 1). Chi-square analyses confirmed significant overall host species differences between Red-tailed Hawks and Cooper's Hawks in the prevalence of both parasite groups (*Leucocytozoon*: $\chi^2 = 69.46$, $P < 0.001$; *Haemoproteus*: $\chi^2 = 12.23$, $P = 0.002$). The small sample size for Red-shouldered Hawks did not allow us to run the statistical model for this species.

The logistic regression model for Cooper's Hawks and *Haemoproteus* infections indicated a significant year effect, with more infected birds in 2004 than in 2005 ($\chi^2 = 26.41$, $P < 0.001$), and a significant date effect, with more individuals infected before 15 October than later in the migration season ($\chi^2 = 21.71$, $P < 0.001$). For *Leucocytozoon* infections, we found no significant year effect; however, Cooper's Hawks also showed more *Leucocytozoon* infections early in the migration season ($\chi^2 = 4.92$, $P < 0.026$). No significant ($P \leq 0.05$) age effects or interactions were evident in either model.

Table 1. Prevalence (% infected) of *Haemoproteus* (H) and *Leucocytozoon* (L) in Red-tailed Hawks, Cooper's Hawks, and Red-shouldered Hawks sampled during autumn migration in the Marin Headlands and during winter in the Central Valley of California.

SPECIES	LOCATION	YEAR	AGE	N	H	L
Red-tailed Hawk	Marin Headlands	2004	Juvenile	143	67	29
			Adult	9	78	22
	Central Valley	2005	Juvenile	28	29	29
			Adult	3	0	0
		2004	Juvenile	60	47	8
			Adult	47	43	11
2005	Juvenile	27	22	26		
	Adult	6	33	17		
Cooper's Hawk	Marin Headlands	2004	Juvenile	29	90	66
			Adult	2	100	5
	2005	Juvenile	66	33	65	
		Adult	5	20	6	
Red-shouldered Hawk	Marin Headlands	2004	Juvenile	4	25	0
			Juvenile	2	0	0
	Central Valley	2004	Juvenile	5	20	40
			Adult	4	0	0
		2005	Juvenile	2	0	0
			Adult	4	25	0

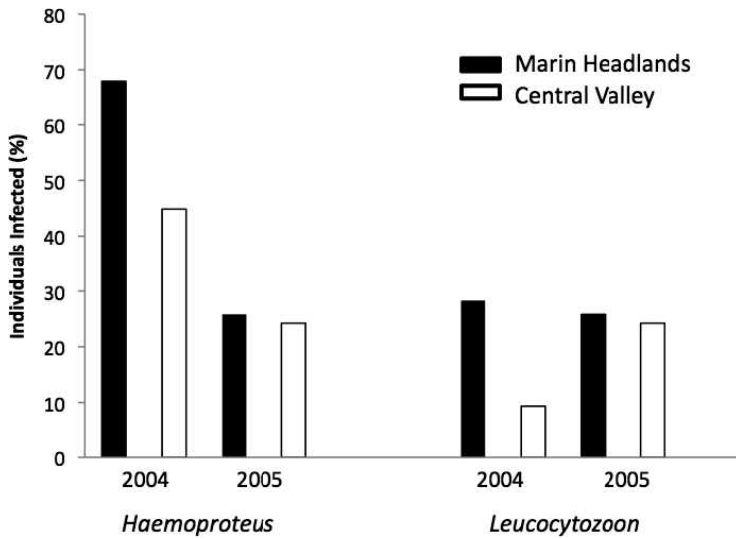


Figure 2. Blood-parasite prevalence in Red-tailed Hawks sampled in 2004 and 2005 during autumn migration in the Marin Headlands and during winter in the Central Valley, California.

For Red-tailed Hawks and *Haemoproteus* prevalence, the logistic regression model indicated significant interactions between year and site ($\chi^2 = 7.11$, $P = 0.007$) and between year and date ($\chi^2 = 10.24$, $P = 0.0014$). The first interaction term indicated higher infection rates at the Marin Headlands in 2004 than in 2005, whereas Central Valley birds were similarly infected in both years (Fig. 2). The second interaction term indicated that Red-tailed Hawks captured after 15 October during the 2004 migration season were significantly more likely to be infected with *Haemoproteus* than those captured before 15 October in the same season; however, the opposite was true in 2005 (Fig. 3). No other significant main effects or interactions were evident in either model.

For Red-tailed Hawks and *Leucocytozoon* prevalence, we again found significant interactions between year and site ($\chi^2 = 6.89$, $df = 1$, $P = 0.008$) and between year and date ($\chi^2 = 5.28$, $P = 0.022$). In this case, infection prevalence did not differ between years in the Marin Headlands, whereas individuals were more infected in 2005 than in 2004 in the Central Valley (Fig. 2). Interestingly, though, we found the same seasonal trend for *Leucocytozoon* infections as for *Haemoproteus* (Fig. 3).

The ANOVA model of Red-tailed Hawk body condition indicated significant main effects for sex ($F_{1,272} = 44.88$, $P < 0.001$), site ($F_{1,272} = 23.99$, $P < 0.001$), and *Haemoproteus* infection status ($F_{1,272} =$

5.16, $P = 0.024$), as well as significant interactions between sex and site ($F_{1,272} = 14.12$, $P < 0.001$) and between sex and *Haemoproteus* infection status ($F_{1,272} = 6.06$, $P = 0.014$). Given the strong significance of sex as a main effect and two relevant interaction terms, we also ran separate sex-specific analyses with all other explanatory variables and relevant interactions included in each model. For female Red-tailed Hawks, we found only a site effect, which indicated that females captured in the Marin Headlands were in poorer condition than those captured in the Central Valley ($F_{1,118} = 33.38$, $P < 0.001$). For males, we did not find a site effect ($F_{1,153} = 0.75$, $P = 0.38$), but males captured before 15 October were in better condition than those captured later in the season ($F_{1,153} = 6.61$, $P = 0.011$). In addition, males with a *Haemoproteus* infection were in poorer condition than those without such an infection ($F_{1,153} = 13.35$, $P < 0.001$). We saw no evidence of a change in body condition with *Leucocytozoon* infection, between years, or between age groups.

DISCUSSION

Overall, 50% of the hawks from this study were infected with *Haemoproteus* and 30% harbored *Leucocytozoon* infections. Although we sequenced only a random subset of individuals, our results suggested that the prevalence of *Plasmodium* infections was likely absent or very low. We did not sequence every individual for which a positive *Haemoproteus* or *Plas-*

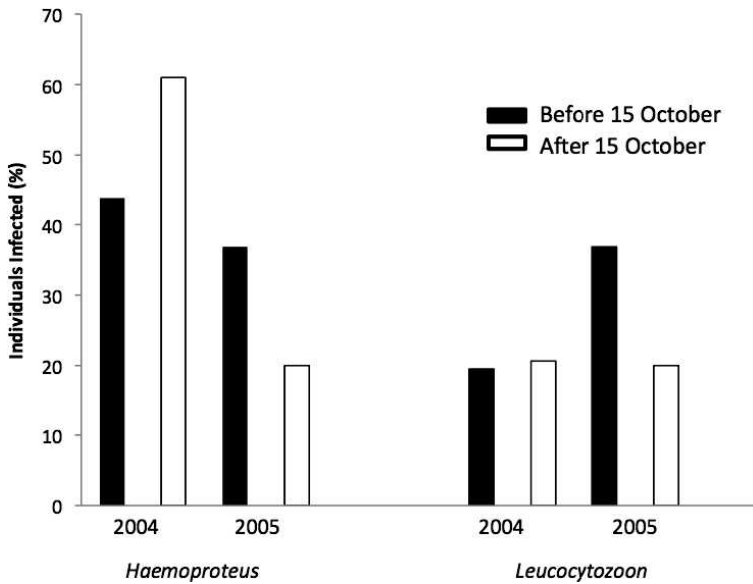


Figure 3. Seasonal variation of blood-parasite prevalence in Red-tailed Hawks sampled in 2004 and 2005 during autumn migration in the Marin Headlands, California.

modium infection was indicated, because we believe the extent of variation was adequately confirmed by the fact that 54 individuals showed the same *Haemoproteus* lineage. Greiner et al. (1975) and Ziman et al. (2004) also recorded high prevalences of *Haemoproteus* and *Leucocytozoon* via microscopy, but no *Plasmodium* parasites in diurnal raptors on the West Coast.

We found that collection year accounted for significant differences in the prevalence of *Haemoproteus* among Red-tailed and Cooper's hawks (Table 1). For both species, *Haemoproteus* prevalence was much higher in 2004 than in 2005, and among Central Valley Red-tailed Hawks, *Leucocytozoon* prevalence was higher in 2005 than in 2004. Other studies have noted yearly differences in parasite prevalence and have attributed this temporal variation to variation in vector abundance (Greiner et al. 1975, Van Riper et al. 1986, Sol et al. 2000, Scheuerlein and Ricklefs 2004) and numbers of potential host species (Ricklefs et al. 2005).

We suspect, however, that the significant differences in *Haemoproteus* prevalence between years most likely are related to the conspicuously different capture rates for Red-tailed Hawks in the Marin Headlands in the two years. In 2005, GGRO volunteers captured only 12 Red-tail Hawks after 15 October, compared to 109 captured during the same period the previous year, and the overall capture rate for Red-tailed Hawks was unusually low that year ($n = 121$, including hawks not tested for blood

parasites) when compared to the mean capture rate of 303 per yr (data from 22 yr of collection; GGRO unpubl. data). The reason for the reduced number of Red-tailed Hawks in 2005 is unknown and may reflect a variety of factors beyond the scope of this study. Due to the unusually low number of birds captured in 2005, we propose that future research hypotheses stemming from this work should be based on only the 2004 data.

Within the subset of Red-tailed Hawks from the Marin Headlands, we found that the prevalence of *Haemoproteus* and *Leucocytozoon* increased significantly during the second half of the 2004 (but not 2005) migration season (Fig. 3). We observed the opposite pattern (significantly more infected before 15 Oct) for both parasite species among Cooper's Hawks. Variation in blood-parasite prevalence between early and late migrants has been documented in other avian studies. For example, Rintamäki et al. (1998) found a pattern in Willow Warblers (*Phylloscopus trochilus*), in which individuals infected with *Haemoproteus* migrated earlier than those infected with *Leucocytozoon*. That study also documented a possible trend in which individuals infected with *Haemoproteus* were captured early and the number of infected individuals decreased with time, whereas the number of *Leucocytozoon* infections increased with time and was highest at the end of migration. The study by Rintamäki et al. (1998) showed differential tim-

ing in the migration of birds infected with the two blood parasites, whereas in our study high infection rates for the two parasites occurred during the same period; i.e., either before or after 15 October, depending on the year and/or hawk species.

Phalen et al. (1995) showed that Sharp-shinned Hawks (*Accipiter striatus*) and Cooper's Hawks caught late in spring migration had higher parasite prevalences than individuals captured earlier. The authors attributed this phenomenon to spring relapse, which is a seasonal increase in parasite intensity that occurs at the onset of breeding, perhaps initiated by hormone changes and the extra energy burdens of reproduction (Phalen et al. 1995, Schrader et al. 2003). However, we observed the same phenomenon during autumn migration among Red-tailed Hawks, when there is no reproductive stress to induce a spring relapse. Therefore, one hypothesis for the results seen in 2004 is that, among Red-tailed Hawks, the stress of migration alone may be sufficient to weaken the immune system enough to allow parasite infections to persist or worsen during autumn, perhaps causing the infected individuals to migrate behind healthier unparasitized birds. We did not observe the same pattern in Cooper's Hawks, however. Hence, an alternative explanation may be that, both within and among species, the migrant birds comprise individuals from different source areas that became infected at different locations. Indeed, a recent study by Hull et al. (2009) showed that GGRO migrants caught from 15 August to 30 September appeared to be local dispersers, whereas those caught from 1 October to 30 November most likely included a mixture of birds from California and the Intermountain West. It is also known that there are significant genetic differences among populations of Red-tailed Hawks (Hull et al. 2008). Thus, it is possible that the higher prevalence of *Haemoproteus* in late-season migrants may be attributed to their different sites of origin.

The breeding grounds of the birds may not necessarily be the site of parasite transmission, however. Hasselquist et al. (2007) found that transmission of *Haemoproteus* occurred on migratory stopover sites and wintering grounds, such that the vector location drove the observed blood-parasite prevalence. Manwell (1955) also found completely different rates of infection among eastern and western American Robins (*Turdus migratorius*), which he believed to be a function of differing vector distributions. Accordingly, further research to confirm the source-population dynamics of Marin Headlands

migrants and associated parasite transmission vectors may help explain the patterns we observed.

We found no significant differences in parasite prevalence between juveniles and adults of the three species analyzed. Higher parasite prevalence in adults has been recorded in some avian-parasite studies (Davidar and Morton 1993, Garvin and Greiner 2003), but not in others (Rintamäki et al. 1998, Garvin et al. 2003, Ricklefs et al. 2005). Although we detected no age-related differences in parasite prevalence, we were unable to examine parasite intensity (parasitemia). Typically, juveniles experience a more severe acute-phase infection than adults, because they have not had time to develop an acquired immunity (Hunter et al. 1997, Dawson and Bortolotti et al. 2000, Sol et al. 2003, Stjernman et al. 2004). Thus, analyzing only differences in prevalence data between age classes may underestimate the relative effects of blood parasites on juveniles and adults (Sol et al. 2003, Leppert et al. 2004).

Finally, we found that female Red-tailed Hawks in the Marin Headlands averaged significantly lower body condition index scores than those in the Central Valley (also see Pitzer et al. 2008). Although body condition scores between sampling sites could be explained by numerous factors, we assume that hawks with a lower mass to wing length residual score from the same sample site is an indication of poorer health (Hull et al. 2006). Several studies have reported effects of parasitism on body condition indices, and indeed we did find a significant effect in migrating males (Dawson and Bortolotti 2000, Schrader et al. 2003, Stjernman et al. 2004, Dyrce et al. 2005). Males tested prior to 15 October were in better condition than those captured after 15 October, suggesting that early migrants have better health. Due to the sex discrepancy, however, it is difficult to generalize concerning how these parasites may affect their hosts. We also acknowledge that using residuals from a mass-wing length regression as an index of body condition is a relatively coarse tool for revealing the complexities of physiological interactions between parasites and the body condition of their hosts (Green 2001, Schulte-Hostedde et al. 2005), which may have precluded our uncovering relatively subtle effects.

In conclusion, our study encompasses the largest sample to date of migratory and wintering hawks tested for blood parasites. Our data provide a baseline that will aid future researchers seeking to monitor changes in infectious diseases in hawk populations, which may arise due to factors such as global

climate change and increasing habitat loss in western North America.

ACKNOWLEDGMENTS

We would like to thank the Golden Gate Raptor Observatory and dedicated volunteers for their support and contribution to scientific collection, Josh Hull at the University of California Davis Genetic Resource Conservation Program and Nate Marti at the University of Texas at Austin for statistical guidance, Gediminas Valkiūnas for help with microscopy, and William Riesen from the U.C. Davis Center for Vector Borne Diseases for editing suggestions. We are also grateful to Jeff Smith, Clint Boal, and two anonymous reviewers for insightful comments on the manuscript. R. Sehgal, H. Ishak, and this research were supported in part by an NIGMS MORE Institutional Research and Academic Career Development Award to U.C. Davis and San Francisco State University, grant number K12GM00679.

LITERATURE CITED

- ALLANDER, K. AND G.F. BENNETT. 1995. Retardation of breeding onset in Great Tits (*Parus major*) by blood parasites. *Functional Ecology* 9:677–682.
- BERGER, D.D. AND H.C. MUELLER. 1959. The bal-chatri: a trap for the birds of prey. *Bird-Banding* 30:18–26.
- BLOOM, P.H., W.S. CLARK, AND J.W. KIDD. 2007. Capture techniques. Pages 193–219 in D.M. Bird and K.L. Bildstein [Eds.], *Raptor research and management techniques*. Hancock House Publishers, Blaine, WA U.S.A.
- CLARABUCH, O. AND J. GONZÁLES-SOLÍS. 1998. Parasitism as a migration cost. *Biologia e Conservazione della Fauna* 102:113–117.
- DAVIDAR, P. AND E.S. MORTON. 1993. Living with parasites: prevalence of blood parasites and its effect on survivorship in the Purple Martin. *Auk* 110:109–116.
- DAWSON, R.D. AND G.R. BORTOLOTTI. 2000. Effects of hematozoan parasites on condition and return rates of American Kestrels. *Auk* 117:373–380.
- 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*). *Auk* 122: 558–565.
- FALLON, S.M., E. BERMINGHAM, AND R.E. RICKLEFS. 2003. Island and taxon effects in parasitism revisited: avian malaria in the Lesser Antilles. *Evolution* 57:606–615.
- GARVIN, M.C. AND E.C. GREINER. 2003. Epizootiology of *Haemoproteus danilewskyi* (Haemosporina: Haemoproteidae) in Blue Jays (*Cyanocitta cristata*) in southcentral Florida. *Journal of Wildlife Diseases* 39:1–9.
- , J.P. BASBAUM, R.M. DUCORE, AND K.E. BELL. 2003. Patterns of *Haemoproteus beckeri* parasitism in the Gray Catbird (*Dumetella carolinensis*) during the breeding season. *Journal of Wildlife Diseases* 39:582–587.
- , P.P. MARRA, AND S.K. CRAIN. 2004. Prevalence of hematozoa in overwintering American Redstarts (*Setophaga ruticilla*): no evidence for local transmission. *Journal of Wildlife Diseases* 40:115–118.
- , C.C. SZELL, AND F.R. MOORE. 2006. Blood parasites of Nearctic-Neotropical migrant passerine birds during spring trans-gulf migration: impact on host body condition. *Journal of Parasitology* 92:990–996.
- GODFREY, R.D., JR., A.M. FEDYNICH, AND D.B. PENCE. 1987. Quantification of hematozoa in blood smears. *Journal of Wildlife Diseases* 23:558–565.
- GREEN, A.J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? *Ecology* 82: 1473–1483.
- GREINER, E.C., G.F. BENNETT, E.M. WHITE, AND R.F. COOMBS. 1975. Distribution of the avian hematozoa of North America. *Canadian Journal of Zoology* 53:1762–1786.
- HASSELQUIST, D., Ö. ÖSTMAN, AND J. WALDENSTRÖM. 2007. Temporal patterns of occurrence and transmission of the blood parasite *Haemoproteus payevskyi* in the Great Reed Warbler *Acrocephalus arundinaceus*. *Journal of Ornithology* 148:401–409.
- HULL, J.M., H.B. ERNEST, J.A. HARLEY, A.M. FISH, AND A.C. HULL. 2009. Differential migration between discrete populations of juvenile Red-tailed Hawks (*Buteo jamaicensis*). *Auk* 126:389–396.
- , A.C. HULL, W. REISEN, Y. FANG, AND H.B. ERNEST. 2006. Variation of West Nile virus antibody prevalence in migrating and wintering hawks in central California. *Condor* 108:435–439.
- , ———, B.N. SACKS, J.P. SMITH, AND H.B. ERNEST. 2008. Landscape characteristics influence morphological and genetic differentiation in a widespread raptor (*Buteo jamaicensis*). *Molecular Ecology* 17:810–824.
- HUNTER, B.D., C. ROHNER, AND D.C. CURRIE. 1997. Mortality in fledgling Great-horned Owls from black fly Hematophaga and Leucocytozoonosis. *Journal of Wildlife Diseases* 33:486–491.
- LEPPERT, L.L., S. LAYMAN, E.A. BRAGIN, AND T. KATZNER. 2004. Survey for Hemoparasites in Imperial Eagles (*Aquila heliaca*), Steppe Eagles (*Aquila nipalensis*), and White-tailed Sea Eagles (*Haliaeetus albicilla*) from Kazakhstan. *Journal of Wildlife Diseases* 40:316–319.
- MANWELL, R.D. 1955. Relative incidence of blood parasites in robins of central New York and of the high Rockies. *Journal of Eukaryotic Microbiology* 2:85–88.
- MØLLER, A.P. AND J. ERRITZØE. 1998. Host immune defense and migration in birds. *Evolutionary Ecology* 12: 945–953.
- NEWTON, I. 1979. *Population ecology of raptors*. Buteo Books, Vermillion, SD U.S.A.
- PHALEN, D.N., C. TAYLOR, S.W. PHALEN, AND G.F. BENNETT. 1995. Hemograms and hematozoa of Sharp-shinned (*Accipiter striatus*) and Cooper's hawks (*Accipiter cooperii*) captured during spring migration in northern New York. *Journal of Wildlife Diseases* 31:216–222.
- PITZER, S., J. HULL, H. ERNEST, AND A. HULL. 2008. Sex determination of three raptor species using morphology and molecular techniques. *Journal of Field Ornithology* 79:71–79.

- REMPLE, J.D. 2004. Intracellular hematozoa of raptors: a review and update. *Journal of Avian Medicine and Surgery* 18:75–88.
- RICKLEFS, R.E., B.L. SWANSON, S.M. FALLON, A. MARTÍNEZ-ABRAÍN, A. SCHEUERLEIN, J. GRAY, AND S.C. LATTA. 2005. Community relationships of avian malaria parasites in southern Missouri. *Ecological Monographs* 75:543–559.
- RINTAMÄKI, P.T., M. OJANEN, H. PAKKALA, AND M. TYNJÄLÄ. 1998. Blood parasites of migrating Willow Warblers (*Phylloscopus trochilus*) at a stopover site. *Canadian Journal of Zoology* 76:984–988.
- , E. HUHTA, J. JOKIMÄKI, AND D. SQUIRES-PARSONS. 1999. Leucocytozoonosis and trypanosomiasis in redstarts in Finland. *Journal of Wildlife Diseases* 35:603–607.
- SAS INSTITUTE. 1999. SAS user's guide. SAS Institute Inc., Cary, NC U.S.A.
- SCHEUERLEIN, A. AND R.E. RICKLEFS. 2004. Prevalence of blood parasites in European passeriform birds. *Proceedings of the Royal Society B: Biological Sciences* 271:1363–1370.
- SCHRADER, M.S., E.L. WALTERS, F.C. JAMES, AND E.C. GREINER. 2003. Seasonal prevalence of a haematozoan parasite of Red-bellied Woodpeckers (*Melanerpes carolinus*) and its association with host condition and overwinter survival. *Auk* 120:130–137.
- SCHULTE-HOSTEDDE, A.I., B. ZINNER, J.S. MILLAR, AND G.J. HICKLING. 2005. Restitution of mass-size residuals: validating body condition indices. *Ecology* 86:155–163.
- SEHGAL, R.N.M., A.C. HULL, N.L. ANDERSON, G. VALKIUNAS, M.J. MARKOVETS, S. KAWAMURA, AND L.A. TELL. 2006. Evidence for cryptic speciation of *Leucocytozoon* spp. (Haemosporida, Leucocytozoidae) in diurnal raptors. *Journal of Parasitology* 92:375–379.
- SMITH, R.B., E.C. GREINER, AND B.O. WOLF. 2004. Migratory movements of Sharp-shinned Hawks (*Accipiter striatus*) captured in New Mexico in relation to prevalence, intensity, and biogeography of avian hematozoa. *Auk* 121:837–846.
- SOL, D., R. JOVANI, AND J. TORRES. 2000. Geographical variation in blood parasites in feral pigeons: the role of vectors. *Ecography* 23:307–314.
- , ———, AND ———. 2003. Parasite mediated mortality and host immune response explain age-related differences in blood parasitism in birds. *Oecologia* 135:542–547.
- STJERNMAN, M., L. RÄBERG, AND J.A. NILSSON. 2004. Survival costs of reproduction in the Blue Tit (*Parus caeruleus*): a role for blood parasites? *Proceedings of the Royal Society B: Biological Sciences* 271:2387–2394.
- SWOFFORD, D.L. 2002. PAUP* phylogenetic analysis using parsimony (* and other methods), version 4.0b10. Sinauer Associates, Sunderland, MA U.S.A.
- SZYMANSKI, M.M. AND I.J. LOVETTE. 2005. High lineage diversity and host sharing of malarial parasites in a local avian assemblage. *Journal of Parasitology* 91:768–774.
- VALKIUNAS, G. 2005. Avian malaria parasites and other haemosporidia. CRC Press, Boca Raton, FL U.S.A.
- VAN RIPER, C., III, S.G. VAN RIPER, M.L. GOFF, AND M. LAIRD. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecological Monographs* 56:327–344.
- ZIMAN, M., A. COLAGROSS-SCHOUTEN, S. GRIFFEY, AND B. STEDMAN. 2004. *Haemoproteus* spp. and *Leucocytozoon* spp. in a captive raptor population. *Journal of Wildlife Diseases* 40:137–14.

Received 16 May 2008; accepted 14 April 2010
Associate Editor: Jeff P. Smith