EPIZOOTIOLOGY OF HAEMOPROTEUS DANILEWSKYI (HAEMOSPORINA: HAEMOPROTEIDAE) IN BLUE JAYS (CYANOCITTA CRISTATA) IN SOUTHCENTRAL FLORIDA

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Source: Journal of Wildlife Diseases, 39(1) : 1-9

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-39.1.1

Journal of Wildlife Diseases, 39(1), 2003, pp. 1–9

EPIZOOTIOLOGY OF *HAEMOPROTEUS DANILEWSKYI* (HAEMOSPORINA: HAEMOPROTEIDAE) IN BLUE JAYS (*CYANOCITTA CRISTATA*) IN SOUTHCENTRAL FLORIDA

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ABSTRACT: Prevalence and density of *Haemoproteus danilewskyi* was studied in a population of free-ranging blue jays (*Cyanocitta cristata*) in southcentral Florida (USA) from May 1992 to December 1995. Prevalence of infection was 27% for data combined over years, seasons, ages, and sexes. Prevalence did not vary between sexes or among years, but increased with age and varied with season, being highest in June–July and lowest in November–January. Parasite density did not vary between sexes or among seasons, but was higher in younger birds when controlling for season. To determine periods of natural transmission, seasonal patterns of infection were compared with previous month abundance of the biting fly vectors. Mean monthly prevalence of *H. danilewskyi* in older jays was positively correlated with previous month abundance of *Culicoides edeni* and *C. arboricola,* both capable of sporogonic development of *H. danilewskyi.*

Key words: Blood parasites, blue jay, *Culicoides,* epidemiology, *Haemoproteus.*

INTRODUCTION

Haemoproteus spp. are common arthropod-borne blood parasites of many species of wild birds. Although the impact of these infections on passerine birds is potentially great (van Riper et al., 1986; Atkinson and van Riper, 1991), little is known of the effects of blood parasites at either the individual or population level. Comparative studies suggest that hematozoan infections have little debilitating effect (Ashford, 1971; Bennett et al., 1988), however, such infections may contribute to population regulation in subtle ways. For example, infection may render hosts more susceptible to other mortality factors, including other pathogens or predators. Furthermore, detection of most population level effects requires long-term monitoring and detailed demographic studies of host, parasite, and arthropod vector. However, during studies of the impact of parasites on their hosts, many workers lack a thorough understanding of both the host and parasite species (Endler and Lyles, 1989). This is especially true of avian hematozoa of the genus *Haemoproteus*, a genus that has been the focus of many blood parasite surveys, but rarely the focus of either ecologic or pathologic studies.

During a preliminary survey of the blood parasites of blue jays (*Cyanocitta cristata*) from May through July 1992 at Archbold Biological Station in southcentral Florida (USA), 40% of the individuals were found to be infected with *Haemoproteus danilewskyi.* As the groundwork for a study of the pathologic effects of these infections, we examined the dynamics and the natural transmission of *H. danilewskyi* in a population of free-ranging blue jays in southcentral Florida. Specifically, we examined the effect of age, sex, and season on the prevalence and density of infection and compared the seasonal abundance of three *Culicoides* spp. capable of sporogonic development of *H. danilewskyi* infections to the seasonal prevalence and density of infection in blue jays.

METHODS

Study site

We conducted field work at Archbold Biological Station (27°10′N, 81°21′W) at the southern end of the Lake Wales Ridge in Highlands County, southcentral Florida. The 2,024 ha, xeric upland preserve is a relict ancient dune system comprising of a mosaic of seven vegetation

types that vary with elevation across a range of 35–65 m (Abrahamson et al., 1984).

At higher elevations where the sandy soil of the ridge is well-drained with little or no standing water, three vegetation associations are common. Southern ridge sandhill habitat is dominated by 8–10 m slash pine (*Pinus elliottii*), 3–4 m oaks (*Quercus laevis, Q. geminata,* and *Q. myrtifolia*), scrub hickory (*Carya floridana*), and scrub palmetto (*Sabal etonia*). Sand pine scrub is predominantly an overstory of mature sandpine (*Pinus clausa*), of varying height, reaching 10 m or more. Common understory and shrub species include *Q. myrtifolia, Q. inopina, C. floridana, S. etonia,* and rosemary (*Ceratiola ericoides*). The scrubby flatwood habitat is dominated by either 1–2 m *Q. inopina* or *Q. geminata.* Other common species are scrub palmetto, saw palmetto (*Serenoa repens*), and fetterbush (*Lyonia lucida*). Trees are sparse, with slash pines being dominant. Because fire is an important ecologic factor in these habitats, land management includes prescribed burns and height of all vegetation associations vary with time.

At lower elevations standing water occurs in man-made drainage ditches, bayheads, ephemeral ponds, and swales during the summer rainy season and in cattle ponds and a 36 ha sinkhole lake throughout the year. Bayhead habitat is found in low, poorly-drained areas and is dominated by several species of bay trees (*Persia borbonia, Gordonia lasianthus,* and *Magnolia virginiana*) that grow to approximately 12 m in height. Swales and seasonal ponds, where standing water is frequent during the summer rainy season, are often dominated by cutthroat grass (*Panicum abscissum*) and Edison's St. John's wort (*Hypericum edisonianum*), although species diversity varies greatly. Surrounding these ephemeral wetlands are flatwoods dominated by scrub pine, saw palmetto, gallberry (*Ilex glabra*), and wiregrass (*Aristida stricta*). Botanical nomenclature follows Wunderlin (1982).

The climate is subtropical with a rainy season during the hot summer months and dry, mild conditions during the winter months. Average yearly rainfall is 133 cm, with rain falling mostly between June and September and least during winter and spring months. Temperatures below freezing are recorded several times a year between November and February, but last no more than several hours.

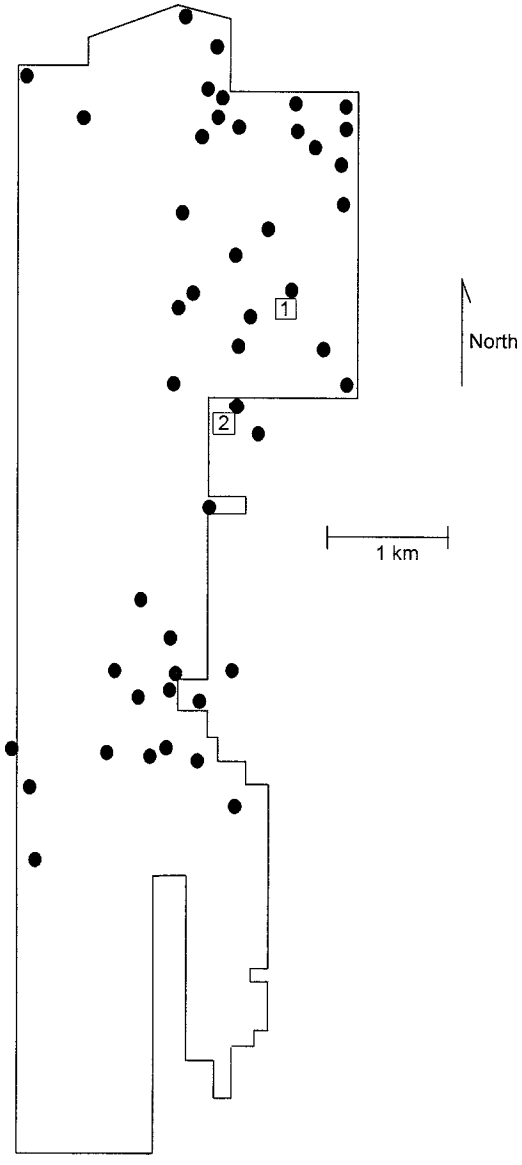

FIGURE 1. Map of bird and *Culicoides* trap sites at Archbold Biological Station (property boundaries indicated). Dots represent bird trap sites. Squares represent vector trap sites (1 and 2).

Epizootiology

To determine influence of age, sex, and season on patterns of infection, we trapped blue jays from May–July 1992, January–August 1993 and 1994, and January–December 1995. From January–August, jays were captured in traps at 46 baited feeding stations (Fig. 1), and less commonly in mist nets in forested areas where jays were more abundant. During August–October, when they were harvesting acorns, blue jays were unlikely to visit baited traps. Therefore, in 1995, we sampled jays during autumn months by shooting and mist netting. Problems associated with the use of multiple sampling

techniques, especially shooting, within a single study may bias results (Fedynich et al., 1995). To control for possible artificial variation in apparent parasite density and prevalence associated with shooting, only blood collected by syringe from the jugular vein prior to the death of shot birds was included in the analyses. Blood also was collected from the jugular vein of nestlings in 1994–95.

In 1992 and 1993, two thin blood smears were prepared from blood collected via the brachial vein of each bird captured. From 1994–95 thin blood smears were prepared from blood collected via the jugular vein with a 1 cc syringe rinsed with 50 mM ethylenediaminetetraacetic acid and equipped with a 27 G ½ inch needle. Thin blood smears were fixed in absolute methanol for several minutes and later stained with Wright-Giemsa. Smears were viewed under 100× oil immersion until an estimated 100,000 red blood cells (RBCs) were examined for each bird and density of infection was determined by estimating the number of infected RBCs per 10,000. Representative slides from the specimens under study were deposited in the US National Parasite Collection (Beltsville, Maryland, USA; Accession numbers 091708-10).

We assigned blue jays to four age categories determined by color and pattern of primary and secondary wing feathers and their associated coverts (Dater, 1970; Bancroft and Woolfenden, 1982; Tarvin and Woolfenden, 1999): hatching-year (HY) for birds in their calendar year of hatching; one year (1YR) for birds in their second calendar year; after one year (A1Y) for birds after their second calendar year; and age unknown (AHY). Because individuals in their second calendar are difficult or impossible to distinguish from older birds after August, all unbanded nonhatching-year birds captured in the fall were classified as "after hatching-year" (AHY).

We tested for differences in the prevalence of infection among ages using chi-square contingency analysis and for differences in mean density of infection among ages using a Kruskal-Wallis one-way analysis of variance. Given the 12–14 day prepatent period of *H. danilewskyi,* nestlings were not likely to have detectable infections before fledging at 17–21 days of age; therefore nestlings were excluded from these analyses.

For these and all subsequent analyses, a P value ≤ 0.05 was considered significant. All statistical analyses were performed with SPSS (SPSS Inc., 1994).

Sex was determined by laparotomy, presence of a brood patch, or behavior at the nest. Jays were anesthetized with isoflurane (Aerane®, Il Sung Co. Korea) and restrained. An incision was made on the left side between the ribs to observe the gonads. Testis size was measured and follicle size of ovaries was estimated. Care was taken to ensure that the jays were handled humanely and allowed to recover fully from anesthesia prior to being released, approximately 30 min after laparotomy. Because females incubate while males provide them with food, we also were able to determine sex of previously color banded individuals through observation at the nest. We tested for differences in the prevalence of infection between sexes using chi-square contingency analysis and for differences in mean density between sexes using a Wilcox Rank Sum test.

Because transmission and relapse of blood parasite infections in birds may occur seasonally in association with breeding (Haberkorn, 1968), we searched for seasonal differences in prevalence of infection within years by dividing each year into five seasons based on observations of the annual cycle of blue jays at Archbold (K. A. Tarvin, unpubl. data). The seasons were as follows: 1) prebreeding, February–March, 2) breeding, April–May, 3) juvenile dependence upon adults for nutrition, June–July, 4) acorn harvesting, August–October, 5) winter, November–January. During the prebreeding season, jays become vocal and conspicuous. In February courtship begins and in late March nest building is initiated and continues into June and July, with the bulk occurring in April and May. Nearly all nests found during 1994 and 1995 were initiated during these 2 mos. From June through July, young have left the nest, but remain nutritionally dependant on the parents. During August, September, and October, jays harvest and cache acorns for a winter food reserve. From November through January, blue jays are quiet and inconspicuous. Because of their preoccupation with acorns in the fall and the quiet, secretive behavior during the winter, jays are difficult to capture from August through January and, therefore, sample sizes during these periods are relatively small. We tested for differences in the prevalence of infection among seasons using chi-square contingency analysis. We used a Kruskal-Wallis one-way analysis of variance to assess the relationship of monthly prevalence of infection for all ages and mean density of infection of 1YR birds with previous month mean vector abundance.

RESULTS

Epizootiology

We collected 786 blood samples from 539 blue jays captured at 44 sites at Archbold Biological Station from 1992–95. Of

TABLE 1. Prevalence of infection of *H. danilewskyi* in blue jays relative to age for the entire year, and during the spring only, 1992–95.

	January–December		February–May	
Age[a]	*n*	% infected	*n*	% infected
HY	94	23	—	—
1YR	153	17	80	16
A1Y	375	38	197	33

[a] HY=hatching year; 1YR=1 year; A1Y=after 1 year.

the 539 jays, 159 were sampled more than once. Because subsequent samples from an individual were collected at different ages and often during different seasons, each sample was considered independent. Prevalence of *H. danilewskyi* was 27% for all samples combined. Other hematozoa observed during this study include *Plasmodium circumflexum* from one jay, *Trypanosoma avium* from two jays, and unidentified microfilariae from three jays.

The number of jays sampled and prevalences of *H. danilewskyi* varied across trap sites. Among sites, sample sizes varied from one to 144 and prevalences varied from zero to 67%. Although prevalences of infection varied among trap sites, all sites were combined because of sample size limitations and problems inherent with interpreting habitat effects.

Prevalence was significantly higher in older than in younger birds ($\chi^2=24.4$, $P<0.001$, Table 1). We controlled for season by comparing birds captured only during the pre-breeding (February–March) and breeding (April–May) months. Hatch year birds were excluded from the analysis because they did not leave the nest until June and July.

Sex was determined for 137 jays. Thirty-six (57%) of 63 females and 43 (58%) of 74 males were infected. No significant difference in prevalence was detected between sexes ($\chi^2=0.324$, $P=0.579$, df=1). To control for season and age, the effect of sex on prevalence was examined among birds of the same age class captured from February through May. Again, no significant differences were detected for 1YR

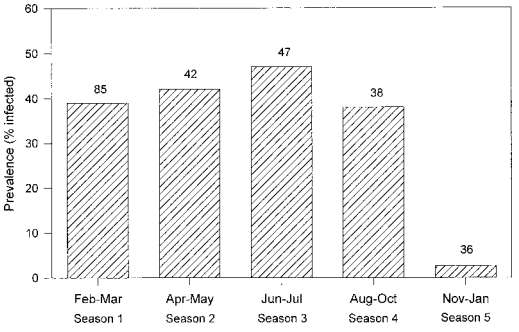

FIGURE 2. Seasonal prevalence of infection in A1Y birds 1992–95. Numbers above bars indicate sample size.

birds ($\chi^2=1.02$, $P=0.31$, df=1) or A1Y birds ($\chi^2=0.48$, $P=0.49$, df=1).

Prevalence did not vary significantly among years ($\chi^2=3.89$, $P=0.27$, df=3). Based on the 248 samples from A1Y birds, prevalence varied significantly among seasons ($\chi^2=25.49$, $P<0.001$, df=4, Fig. 2). Prevalence was highest during June–July (47%), and was lowest during November–January, when only one of 36 samples (3%) was positive. We found no significant variation from February–October.

We also found a significant effect of season on prevalence during the first year of life ($\chi^2=13.30$, $P=0.021$, df=4, Fig. 3). Prevalence in HY birds during June–July, when most birds fledged, was relatively low (20%). A greater percentage of fledglings (37%) sampled during August–October were infected. During their first prebreeding season (February–March), prevalence dropped to 7%, increased sharply

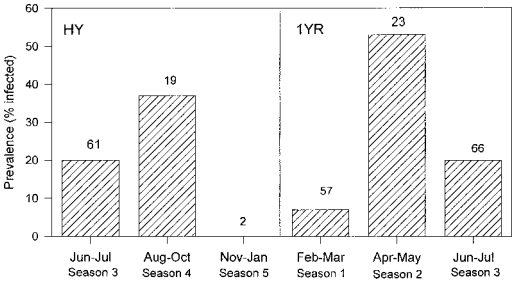

FIGURE 3. Seasonal prevalence of infection in HY birds (left) and 1YR birds (right), 1992–95. Numbers above bars indicate sample size.

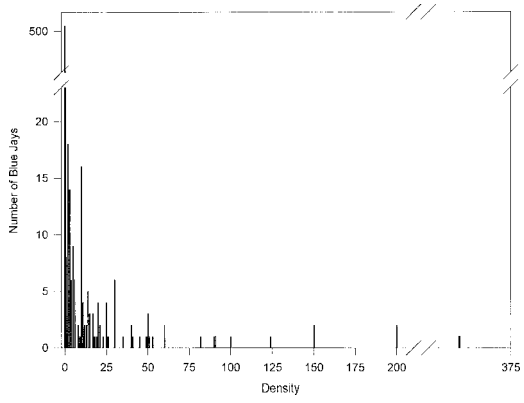

FIGURE 4. Frequency distribution of parasite density in blue jays, 1992–95. Density was measured as number of infected erythrocytes per 10,000 erythrocytes.

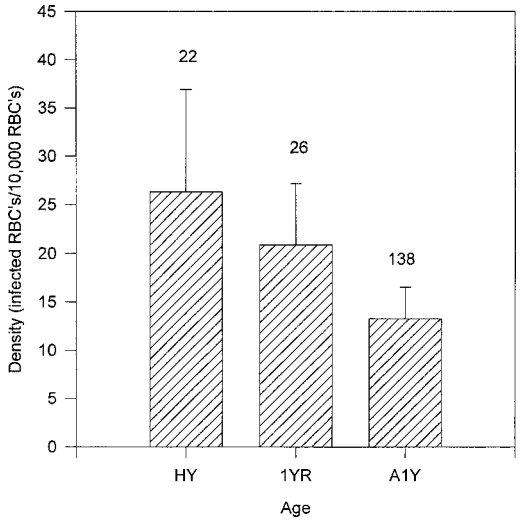

FIGURE 5. Mean density of infection, infected birds only, relative to age across all seasons, 1992–95. Numbers indicate sample size. Bars indicate standard error.

to 53% during the breeding season (April–May), then decreased to 20% after the breeding season in June–July.

Parasite density of infection followed a negative binomial distribution (Fig 4). Most infected jays had very low parasitemias and only a few had very high parasite densities.

When parasite density was compared among all groups, we found no significant variation, although there was a trend toward decreasing variation with host age (H=4.49, P=0.11, df=2, Fig. 5). To control for possible effects of season on density, samples collected February–May were examined. Because HY birds were not sampled until after they left the nest in June and July, they were excluded from this analysis. We found 1YR birds had a significantly higher parasite density (n=13, $\bar{x}$=24.4, range <1–124) than A1Y birds (n=65, $\bar{x}$=13.5, range <1–200, U=659.0, P=0.050).

No significant difference in parasite density was detected between females and males (T=4493.5, P=0.866, Fig. 6A). To control for season and age, we tested for the effect of sex within age groups for jays captured from February–May. Of the 1YR jays that were infected, mean density of infection was not significantly different between males ($\bar{x}$=17.3, SD=37.50) and females ($\bar{x}$=18.5, SD=13.25, t=21.0, P=0.905, Fig. 6B). Similarly, of the A1Y jays that were infected, mean density was not significantly different between females ($\bar{x}$=12.2, SD=28.7) and males ($\bar{x}$=14.2, SD=28.4, t=502.5, P=0.968, Fig. 6B).

No significant variation in mean density of infection was found among seasons in 1YR (H=3.86, P=0.425, df=4) or A1Y birds (H=5.07, P=0.280, df=4). Mean parasite density of 1YR birds did not differ significantly among April–May ($\bar{x}$=30, range 1–100), June–July ($\bar{x}$=28.9, range

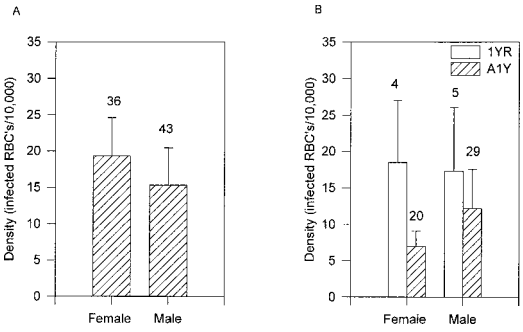

FIGURE 6. Density of infection of males and females. Because there were no between-year differences, years were combined. Bars indicate standard error. A) across all seasons B) February through May.

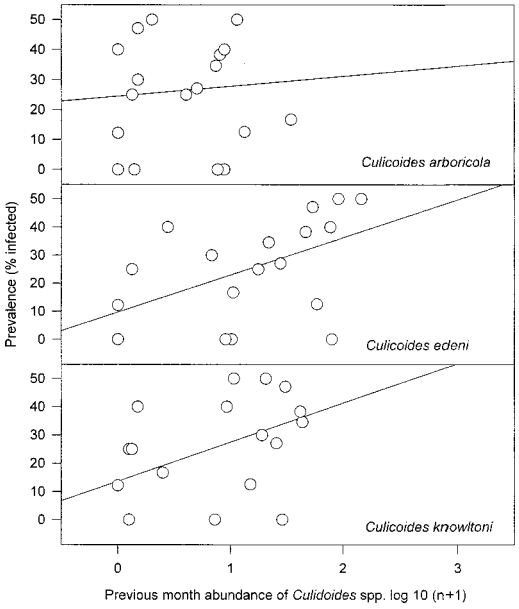

FIGURE 7. Monthly prevalence of infection of *H. danilewskyi* in blue jays in relation to mean *C. arboricola, C. edeni,* and *C. knowltoni* abundance during preceding month, 1994–95.

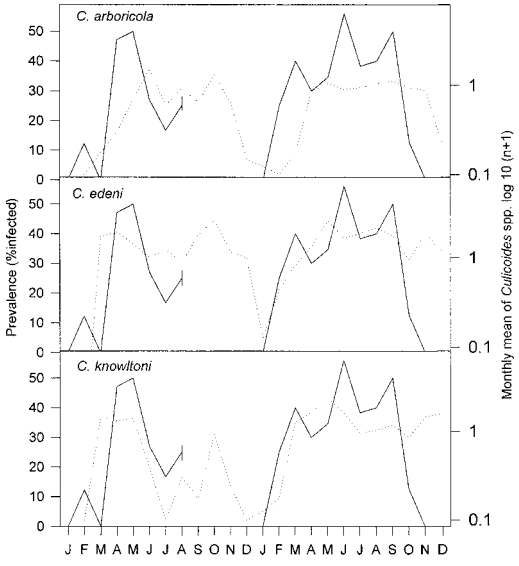

FIGURE 8. Mean monthly prevalence of infection of *H. danilewskyi* relative to *C. arboricola, C. edeni,* and *C. knowltoni* abundance, 1994–95. ——— prevalence of infection; – – – abundance of *Culicoides* spp.

<1–200), or August–October ($\bar{x}$=5.7, range <1–19).

In A1Y birds parasite density ranged from <1–200 ($\bar{x}$=19.5) during February–March. During April–May, density ranged from <1–50 ($\bar{x}$=7.4), and during June–July, density ranged from <1–360 ($\bar{x}$=12.9). During August–October, density ranged from <1–15 ($\bar{x}$=7.8). Of 36 jays sampled during November–January, only one jay had detectable parasitemia (density <1 infected RBC/10,000).

Mean monthly prevalence of *H. danilewskyi* was positively correlated with abundance of *C. edeni, C. arboricola,* and *C. knowltoni* during the preceding month (Fig. 7). The relationship was significant for *C. edeni* (r_s=0.57, P=0.011) and *C. knowltoni* (r_s=0.54, P=0.016), but not for *C. arboricola* (r_s=0.18, P=0.450). In both 1994 and 1995, *C. edeni* abundance increased prior to the May, June, and July peak in prevalence of *H. danilewskyi,* but followed the initial February peak (Fig. 8). A similar pattern was seen with *C. knowltoni.* Abundance of *C. arboricola* also increased after February in both years but in 1994 did not peak prior to the second peak in parasite prevalence.

To assess the potential influence of vector abundance on parasite density, mean monthly parasite density in 1YR birds during 1994 was compared to the mean vector abundance during the previous month (Garvin and Greiner, 2003). Low reproductive success of blue jays in 1994 prevented a similar analysis for 1995 because of sample size limitations. Peak parasite density was observed during May and was preceded by high monthly averages of *C. edeni* and *C. knowltoni* (Fig. 9). However, overall monthly density of infection was not significantly correlated with previous-month mean abundance in any of the three species.

DISCUSSION

This study represents the first monitoring of *Haemoproteus* infections in wild passerine birds in a subtropical climate. The 27% prevalence of *H. danilewskyi* in blue jays is low relative to other epizooti-

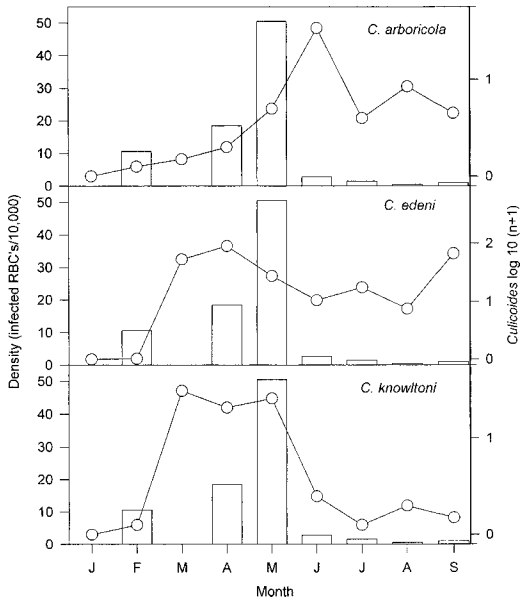

FIGURE 9. Density of infection in 1YR birds (bars) relative to mean monthly *C. arboricola, C. edeni,* and *C. knowltoni* abundance (lines) in 1994.

ologic studies of *Haemoproteus* in wild birds in southern Florida. Atkinson et al. (1983) and Forrester et al. (1974) found up to 90% prevalence in wild turkeys (*Meleagris gallopavo*) at Lykes Fisheating Creek Wildlife Refuge in adjacent Glades County. The relatively low prevalence reported here is not surprising given the shorter period of vector activity reported from Archbold (Garvin and Greiner, 2003) relative to the year-round abundance at Fisheating Creek (Atkinson et al. 1988). Furthermore, overall vector abundance is likely to be lower in the xeric conditions of the relict sand dune habitat of our study site where there are fewer opportunities for breeding of *Culicoides* vectors.

In this study, both prevalence and parasite density varied significantly with age. The observation that probability of blue jays becoming infected increased with age is consistent with other studies of age-related patterns of prevalence and is probably due to increased exposure to biting flies (Bennett and Fallis, 1960; Greiner, 1975). An alternative explanation is that infected fledglings have lower survivorship than uninfected fledglings, thus creating an artificially low prevalence of infection in the set of younger birds sampled. In contrast, younger birds had higher density of infection. These findings lend support to other studies of age-related density of haemosporidian infections which suggest that parasitemia reflects the immune responsiveness of the bird (Chernin, 1952). Because younger birds were less likely to have been exposed to infection previously, their immune response may have been less effective than that of older birds. Blue jays apparently acquired infection after leaving the nest as no infections were detected in nestlings between age day 9 and 17. Although, given the 12–14 day prepatent period, infections acquired in the nest possibly were not detectable before fledging.

Seasonal prevalence and density of *H. danilewskyi* infection may be used to determine periods of relapse and transmission (Janovy, 1966; Greiner, 1975). Relapse, possibly resulting from hormonal changes associated with breeding, involves the movement of latent infections from visceral organ tissue to peripheral circulation (Desser et al., 1968; Haberkorn, 1968; Applegate, 1970; Beaudoin et al., 1971) and provides a source of infection for transmission when vector abundance becomes high. Significant seasonal differences in prevalence were detected in older (A1Y) jays; most notable was the increase from January–February. February–March is a time of courtship for blue jays, and relapse associated with hormonal changes was likely to occur during this time. Significant increase in the prevalence of infection in 1YR jays occurred slightly later during April–May. The later elevated prevalence in young birds may represent initial exposure and infection of young birds or relapsing latent infections. Relapse in 1YR birds may occur after relapse in A1Y birds because first year jays are likely to breed later than older, more experienced birds (Martin, 1995) and, therefore, the hormonal changes and stress associated with

breeding which trigger relapse also are delayed.

Although prevalence of infection in A1Y birds is uniform from February–October, prevalence and density of infection drops dramatically in November and remain low through January. Because vector abundance declined in November and remained low in December and January the low prevalence during this period may result from decreased transmission because of low vector abundance. Alternatively, because jays are generally relatively quiet during December–February, after harvesting acorns and before breeding, perhaps they are under the least physiologic stress and best able to suppress chronic infections.

Although it is not possible to distinguish between relapsing and new infections, high prevalence coupled with high numbers of gametocytes in the peripheral circulation likely reflect newly acquired infections and transmission (Bennett and Fallis, 1960). The presence of seasonal and annual changes in the density of gametocytes in the peripheral circulation within individuals was illustrated in this study by repeatedly sampling infected jays both within and between years. Five A1Y jays with low density infections upon initial sampling had higher parasitemias upon subsequent sampling, followed by a return to the initial level of parasitemia upon third sampling. Increased parasite density may have been a result of reinfection. However, four of the five jays were known to be breeding during the times of elevated parasitemias, suggesting relapse rather than new infections.

Transmission is ultimately dependent on the interactions of arthropod vector species with infected vertebrate hosts. As the biting midge populations increase with rainfall and temperature, relapsing birds are fed upon and infections are transmitted to uninfected birds or previously infected birds, which may become reinfected with subsequent inoculation (Adie, 1925). Janovy (1966) and Bennett and Fallis (1960) found transmission of *Plasmodium* and *Haemoproteus* occurs when adult infections relapse as vector populations increase with the onset of warmer weather. At the same time, young uninfected birds leaving the nest are especially vulnerable to biting flies.

Seasonal patterns of *C. edeni* relative to those of *H. danilewskyi* infections in blue jays, in addition to its relatively high abundance and feeding strata preferences (Garvin and Greiner, 2003) that put it in close spatial association with blue jays, suggest that *C. edeni* is the most important vector of *H. danilewskyi* in southcentral Florida. In both 1994 and 1995, increased abundance of *C. edeni* followed the early February peak in parasite prevalence, likely reflecting relapse of chronic infections, which annually provided a source of infection for transmission. Abundance of *C. edeni* remained high during periods of peak prevalence from February through September and was lowest from November through January. The only infection detected during the winter when *C. edeni* were not detected was an extremely low density, chronic infection in a single individual. Furthermore, annual peaks in *C. edeni* abundance occurred just prior to months of greatest prevalence of infection.

ACKNOWLEDGMENTS

We thank J. Fitzpatrick, D. Forrester, B. Homer, D. Kline, R. Littell, M. Spalding, G. Woolfenden, and K. Tarvin for advice and critical review of this manuscript. We thank K. Tarvin, P. Quintana-Ascencio, P. Midford, R. Littell, and V. Apanius for assistance with statistical analysis. We thank A. Fleischer, S. Lindemann, L. Walton, K. Dayer, J. Jawor, A. Remley, S. Schoech, K. Tarvin, and G. Woolfenden for assistance with field work. W. W. Wirth confirmed *Culicoides* species identifications and shared his knowledge and collections of *Culicoides* from Archbold.

This study was made possible by generous funding from the Department of Pathobiology at the University of Florida, Archbold Biological Station, Frank Chapman Memorial Fund (American Museum of Natural History), National Society of Sigma Xi, and Oberlin College.

LITERATURE CITED

ABRAHAMSON, W. G., A. F. JOHNSON, J. N. LAYNE, AND P. A. PERONI. 1984. Vegetation of the Archbold Biological Station, Florida: An example of the southern Lake Wales Ridge. Florida Scientist 47: 209–250.

ADIE, H. 1925. Nouvelles recherches sur la sporogonie de *Haemoproteus columbae.* Archives de l'Institut Pasteur d'Algérie 3: 9–15.

APPLEGATE, J. E. 1970. Population changes in latent avian malaria infections associated with season and corticosterone treatment. Journal of Parasitology 56: 439–443.

ASHFORD, R. W. 1971. Blood parasites and migratory fat at Lake Chad. Ibis 113: 100–101.

ATKINSON, C. T., E. C. GREINER, AND D. J. FORRESTER. 1983. Experimental vectors of *Haemoproteus meleagridis* Levine from wild turkeys in Florida. Journal of Wildlife Diseases 19: 366–368.

———, AND C. VAN RIPER, III. 1991. Pathogenicity and epizootiology of avian haematozoa: *Plasmodium, Leucocytozoon,* and *Haemoproteus. In* Bird-parasite interactions, J. E. Loye and M. Zuk (eds.). Oxford University Press, Oxford, UK, pp. 20–48.

———, D. J. FORRESTER, AND E. C. GREINER. 1988. Epizootiology of *Haemoproteus meleagridis* (Protozoa: Haemosporina) in Florida: Seasonal transmission and vector abundance. Journal of Medical Entomology 25: 45–51.

BANCROFT, G. T., AND G. E. WOOLFENDEN. 1982. The molt of scrub jays and blue jays in Florida. Ornithological Monographs 29: 1–51.

BEAUDOIN, R. L., J. E. APPLEGATE, D. E. DAVIS, AND R. G. MCLEAN. 1971. A model for the ecology of avian malaria. Journal of Wildlife Diseases 7: 5–13.

BENNETT, G. F., AND A. M. FALLIS. 1960. Blood parasites of birds in Algonquin Park, Canada and a discussion of their transmission. Canadian Journal of Zoology 38: 262–273.

———, J. R. CAINES, AND M. A. BISHOP. 1988. Influence of blood parasites on body mass of passeriform birds. Journal of Wildlife Diseases 24: 339–343.

CHERNIN, E. 1952. The epizootiology of *Leucocytozoon simondi* infections in domestic ducks in northern Michigan. American Journal of Hygiene 56: 39–57.

DATER, E. 1970. Dorsal wing coverts of blue jay (*Cyanocitta cristata*) guide to age. Eastern Bird Banding Association News 33: 129.

DESSER, S. S., A. M. FALLIS, AND P. C. C. GARNHAM. 1968. Relapse in ducks chronically infected with *Leucocytozoon simondi* and *Parahaemoproteus nettionis.* Canadian Journal of Zoology 46: 303–307.

ENDLER, J. A., AND A. M. LYLES. 1989. Bright ideas about parasites. Trends in Evolution and Ecology 4: 246–248.

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

FORRESTER, D. J., L. T. HON, L. E. WILLIAMS, JR., AND D. H. AUSTIN. 1974. Blood protozoa of wild turkeys in Florida. Journal of Protozoology 21: 494–497.

GARVIN, M. C., AND E. C. GREINER. 2003. Ecology of *Culicoides* (Diptera: Ceratopogonidae) in southcentral Florida and experimental *Culicoides* vectors of the avian hematozoa *Haemoproteus danilewskyi* Kruse. Journal of Wildlife Diseases 39: 170–178.

GREINER, E. C. 1975. Prevalence and potential vectors of *Haemoproteus* in Nebraska mourning doves. Journal of Wildlife Diseases 11: 150–156.

HABERKORN, A. 1968. Zur hormonellen beeinflussung von Haemoproteus-infektionen. Zeitschrift für Parasitenkunde 31: 108–112.

JANOVY, J., JR. 1966. Epidemiology of *Plasmodium hexamerium* Huff, 1935, in meadowlarks and starlings of the Cheyenne Bottoms, Barton County, Kansas. Journal of Parasitology 52: 573–578.

MARTIN, K. 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. American Zoologist 35: 340–348.

SPSS, INC. 1994. SPSS for windows. Ver 6.1 Chicago, Illinois.

TARVIN, K. A, AND G. E. WOOLFENDEN. 1999. Blue Jay (*Cyanocitta cristata*). *In* The birds of North America, No. 469, A. Poole and F. Gill (eds.). The Birds of North America, Inc., Philadelphia, Pennsylvania. pp. 1–31.

VAN RIPER, C., III, S. G. VAN RIPER, AND M. LAIRD. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. Ecological Monographs 56: 327–344.

WUNDERLIN, R. P. 1982. Guide to the vascular plants of central Florida. University Presses of Florida, Tampa, Florida, 472 pp.

Received for publication 7 August 2001.