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PREVALENCE OF AVIAN HEMATOZOA IN CENTRAL VERMONT

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ABSTRACT: Peripheral blood smears from 1,547 birds, of 50 species, from 15 families trapped in Northfield, Vermont were examined for hematozoa. Numerous new host–parasite relationships were identified. The prevalence of all species of parasites over the 3 yr of the study was 42.5%. Prevalence of the genera of parasites were: *Leucocytozoon*—36.5%; *Trypanosoma*—7.3%; *Haemoproteus*—6.3%; microfilariae—1.0%; *Plasmodium*—1.0%. Peak prevalence (78.9%) occurred in the first half of July. Peak intensity was seen in the last half of June. Evidence from immature birds suggested that active transmission of all genera of hematozoans took place in the study area. *Leucocytozoon* gametocytes, unlike *Haemoproteus* gametocytes, were detected in smears from birds during all seasons of the year, and showed no period of complete remission. *Trypanosoma* and microfilariae also were seen throughout the year.

INTRODUCTION

Many avian communities have been sampled to better understand the epizootiology of avian hematozoa in North America. Greiner et al. (1975) comprehensively reviewed literature on the prevalence of avian hematozoa as well as unpublished records of the International Reference Centre for Avian Hematozoa, and summarized and tabulated these data by topographical regions. The majority of reports from the northeastern United States, part of Region 5, concentrate on particular species of birds or coastal avian communities. Little information is available on the prevalence of avian hematozoa in inland New England. The few recent studies of inland bird communities within Region 5 (Great Lakes and northeastern Appalachian–Laurentian area) involved sites in southeastern Canada (Bennett et al., 1975), northeastern Canada (Bennett, 1972), and New Jersey (Williams and Bennett, 1978; Kirkpatrick and Lauer, 1985).

The present 3-yr study, conducted in Vermont provided data on the seasonal variation in prevalence of avian hematozoa in migrating and resident birds, and information on the relapse phenomenon associated with species of *Leucocytozoon* and *Haemoproteus*.

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MATERIALS AND METHODS

Field work was conducted in the central Vermont town of Northfield, Washington County, on a hillside bordering a residential area from March 1982 to March 1985. The site was surrounded by brushy fields and second growth forest, and overlooked a river valley. Birds were caught in treadle traps or mist nets and banded with U.S. Fish and Wildlife Service leg bands to permit recognition of previously examined hosts. Each bird was aged and released after a blood sample was taken. The system of avian nomenclature used was that of the American Ornithologists' Union (1983).

Blood samples were obtained from birds using the method of Bennett (1970). Giemsa stained smears were examined for *Trypanosoma* spp., *Leucocytozoon* spp. and microfilariae under low power (100×); and for *Haemoproteus* spp. and *Plasmodium* spp. under oil immersion (1,000×). Each smear was examined for 10–15 min or until 50 oil immersion fields (10,000 erythrocytes) were viewed. Parasites were identified to species, if possible, and intensity was recorded as the number of parasites present/10,000 red blood cells (RBC). Smears with less than one parasite/10,000 RBC were arbitrarily assigned a value of 0.5 parasites/10,000 RBC to permit statistical analysis of the data.

Prevalence and intensity data were grouped into half-month periods (14 to 16 days) and results for each period were summed for the 3 yr of the study. A number of birds were recaptured one or more times during the course of the study. Results from birds recaptured within

TABLE 1. Prevalence of blood parasites in birds of central Vermont, 1982–1985.

Family and species	Total birds examined	No. infected birds[a]	Total infected with:				
			L[b]	H	P	T	M
Columbidae							
Mourning dove, *Zenaida macroura*	27	6	5	0	0	0	1
Hirundinidae							
Cliff swallow, *Hirundo pyrrhonota*	1	1	0	1	0	0	0
Tree swallow, *Tachycineta bicolor*	25	8	5	0	0	3	1
Corvidae							
Blue jay, *Cyanocitta cristata*	163	92	65	35	0	44	4
Paridae							
Black-capped chickadee, *Parus atricapillus*	43	3	3	0	0	1	0
Muscicapidae							
Veery, *Catharus fuscescens*	2	2	1	0	0	1	0
Wood thrush, *Hylocichla mustelina*	1	1	1	0	0	0	1
American robin, *Turdus migratorius*	35	30	30	13	3	4	0
Mimidae							
Gray catbird, *Dumetella carolinensis*	1	1	1	0	0	0	0
Brown thrasher, *Toxostoma rufum*	3	3	2	0	0	2	0
Bombycillidae							
Cedar waxwing, *Bombycilla cedrorum*	4	2	2	0	0	1	0
Sturnidae							
European starling, *Sturnus vulgaris*	17	1	1	0	0	0	0
Vireonidae							
Red-eyed vireo, *Vireo olivaceus*	1	1	1	1	0	1	0
Warbling vireo, *Vireo gilvus*	2	1	0	1	0	0	0
Emberizidae							
Yellow warbler, *Dendroica petechia*	4	1	1	0	0	0	0
Yellow-rumped warbler, *Dendroica coronata*	1	1	1	0	0	0	0
American redstart, *Setophaga ruticilla*	3	2	1	0	0	2	0
Common yellowthroat, *Geothlypis trichas*	8	1	1	0	0	0	0
Scarlet tanager, *Piranga olivacea*	1	1	1	1	0	0	0
Northern cardinal, *Cardinalis cardinalis*	9	5	5	1	0	2	1

TABLE 1. Continued.

Family and species	Total birds examined	No. infected birds[a]	Total infected with: L[b]	H	P	T	M
Rose-breasted grosbeak, *Pheucticus ludovicianus*	2	2	2	0	0	0	0
Rufous-sided towhee, *Pipilo erythrophthalmus*	3	2	2	0	0	1	0
American tree sparrow, *Spizella arborea*	146	46	46	0	0	0	0
Chipping sparrow, *Spizella passerina*	7	5	4	0	0	1	0
Field sparrow, *Spizella pusilla*	9	4	2	0	0	2	1
Fox sparrow, *Passerella iliaca*	1	1	1	1	0	0	0
Song sparrow, *Melospiza melodia*	108	33	15	18	3	3	1
Lincoln's sparrow, *Melospiza lincolnii*	1	1	1	0	0	1	0
White-throated sparrow, *Zonotrichia albicollis*	29	24	18	8	0	4	0
White-crowned sparrow, *Zonotrichia leucophrys*	12	3	1	2	0	0	0
Dark-eyed junco, *Junco hyemalis*	150	73	69	3	1	0	0
Red-winged blackbird, *Agelaius phoeniceus*	52	26	25	2	1	4	1
Common grackle, *Quiscalus quiscula*	102	94	94	9	2	10	3
Brown-headed cowbird, *Molothrus ater*	213	116	112	0	3	5	1
Northern oriole, *Icterus galbula*	2	2	2	1	0	1	0
Fringillidae							
Purple finch, *Carpodacus purpureus*	8	6	2	0	2	3	1
Common redpoll, *Carduelis flammea*	39	2	1	1	0	0	0
Pine siskin, *Carduelis pinus*	25	2	2	0	0	0	0
American goldfinch, *Carduelis tristis*	123	22	12	0	0	12	0
Evening grosbeak, *Coccothraustes vespertinus*	135	30	26	0	0	4	0
Passeridae							
House sparrow, *Passer domesticus*	11	1	0	0	0	1	0
Totals	1,547	658	564	98	15	113	16

[a] Due to birds with multiple infections, totals of parasites present exceeds total number of birds infected.

[b] Abbreviations: L = *Leucocytozoon* spp., H = *Haemoproteus* spp., P = *Plasmodium* spp., T = *Trypanosoma* spp., M = microfilariae.

Negative species (sample size in parentheses): Columbidae, rock dove, *Columba livia* (5); Trochilidae, ruby-throated hummingbird, *Archilochus colubris* (1); Picidae, downy woodpecker, *Picoides pubescens* (3); Troglodytidae, house wren, *Troglodytes aedon* (2); Muscicapidae, ruby-crowned kinglet, *Regulus calendula* (1); Mimidae, northern mockingbird, *Mimus polyglottos* (1); Emberizidae, Nashville warbler, *Vermivora ruficapilla* (2), ovenbird, *Seiurus aurocapillus* (2); Fringillidae, house finch, *Carpodacus mexicanus* (1).

14 days were excluded. Host species diversity in each half-month period was analyzed using the Shannon-Weiner diversity index (Lloyd et al., 1968) to better characterize the host population.

Representative blood films (accession numbers 95942–95953) have been deposited in the International Reference Centre for Avian Haematozoa, Memorial University of Newfoundland, St. John's, Newfoundland A1B 3X9, Canada.

RESULTS

During the 3-yr study, 50 species of birds, representing 15 families were examined. The overall prevalence of hematozoan infections was 42.5% in 1,547 birds. *Leucocytozoon* spp. were seen in 36.5% of the birds, while 7.3% had infections by *Trypanosoma* spp. Species of *Haemoproteus* were noted in 6.3% of the birds and microfilariae in 1.0% of birds. *Plasmodium* spp. infected 1.0%. Hematozoa prevalences differed widely among avian host families. Highest prevalence was found in the Muscicapidae (85%), Corvidae (56%), Emberizidae (51%) and Hirundinidae (35%). Low prevalences in families represented by more than ten samples were found in the Sturnidae (6%), Paridae (7%) and Columbidae (19%) (Table 1).

Leucocytozoon fringillinarum Woodcock, 1910 was the most common species of *Leucocytozoon* encountered. It was present in birds from the Fringillidae, Mimidae, Bombycillidae, Vireonidae, Corvidae, and from five subfamilies of the Emberizidae (Icterinae, Thraupinae, Emberizinae, Cardinalinae, Parulinae). *Leucocytozoon fringillinarum* was found in several avian species (blue jays, scarlet tanagers and brown thrashers) not listed by Bennett et al. (1982) as hosts for this species. *Leucocytozoon majoris* Laveran, 1902 parasitized birds in the Hirundinidae, Corvidae, Muscicapidae, Mimidae, Bombycillidae, Emberizidae (subfamilies Cardinalinae, Emberizinae, and Icterinae). Parasites with the morphology of *L. majoris* were found in several hosts not associated with *L. majoris* by Bennett et al. (1982). These hosts were the tree swallow, brown thrasher, cedar waxwing, rose-breasted grosbeak, northern cardinal, dark-eyed junco, tree sparrow, brown-headed cowbird, common grackle, northern oriole, red-winged blackbird, evening grosbeak and the American goldfinch. *Leucocytozoon dubreuili* Mathis and Leger, 1911 was found in the American robin and wood thrush and the cedar waxwing. *Leucocytozoon dubreuili* was also found in the blue jay and tree swallow, hosts not listed by Bennett et al. (1982) for this species. Gametocytes morphologically identical to *L. sakharoffi* Sambon, 1908 were seen in blue jays as well as three new host species: American robin, evening grosbeak, and northern cardinal. *Leucocytozoon marchouxi* Mathis and Leger, 1911 was found in mourning doves.

Six species of *Haemoproteus* were found, with *H. fringillae/orizivora* most common. *Haemoproteus fringillae/orizivora* was restricted to the Vireonidae and Emberizidae. Gametocytes morphologically similar to *H. picae* Coatney and Roudabush, 1937 were found in many blue jays. American robins hosted *H. fallisi* Bennett and Campbell, 1972, and *H. quiscalus* Coatney and West, 1938 was present in common grackles. Gametocytes of *H. quiscalus* were found in red-winged blackbirds, a host species not listed by Bennett et al. (1982) for *H. quiscalus*.

The most common *Plasmodium* species, *P. nucleophilum* Manwell, 1935, was seen in the American robin, common grackle and red-winged blackbird. *Plasmodium vaughni* Novy and MacNeal, 1904 was seen in the American robin and brown-headed cowbird. *Plasmodium matutinum* (Huff, 1937) and *P. elongatum* Huff, 1930 were identified in the American robin and song sparrow, respectively.

Trypomastigotes with the morphology of *Trypanosoma avium* (Danilewsky, 1885) were encountered in birds from the

families Bombycillidae, Corvidae, Muscicapidae, Mimidae, Vireonidae, Emberizidae, Fringillidae, and Passeridae. Trypanosomes with morphology like that of *T. everetti* Molyneaux, 1973 were seen in the brown-headed cowbird. A third trypanosome, about 25 μm in length and with a subterminal kinetosome was seen in a common grackle.

Data in Table 2 show that there was wide variation in both the species and number of birds examined during the half-month intervals of the study. A high Shannon-Weiner diversity index indicates that a relatively large number of avian species were examined and that the numbers of individuals were relatively evenly distributed among the species. Time periods with low diversity index values indicated samples with few species and/or an inequitable distribution of individuals among the species represented. Highest diversity was present from April through the first half of August, a time period during which the breeding populations were present and that corresponded to high prevalence of infection. Lower diversity was detected during the remainder of the year.

The prevalence of hematozoa was lowest during the late fall, winter and early spring (Table 2). It increased dramatically during April and peaked during the first half of July, when 78.9% of the birds examined harbored one or more hematozoan species. The prevalence of infections in the populations declined steadily after the July peak and precipitously in September. Prevalences fluctuated from 13% to 40% through the winter and early spring.

Early spring resurgence of patent infections followed similar patterns in the three major genera of parasites (Fig. 1). *Leucocytozoon* made the greatest contribution to overall prevalence, with a peak prevalence in the first half of July. Prevalence dropped dramatically during August and was about 20% in birds examined after September. Infections by *Trypanosoma* spp. increased steadily from April to a peak of 33% of birds examined in the latter half of June. Trypanosome infections were encountered commonly in July, declined in August and were seen rarely from September to April. The prevalence of *Haemoproteus* rose from April through June, declined in July, increased again from August to a maximum in the first half of September. Haemoproteid infections were not detected from November through the last half of April despite the presence of suitable hosts (e.g., blue jays) that commonly harbor *Haemoproteus*. The seasonal prevalence of *Leucocytozoon* differed considerably from that of both *Trypanosoma* and *Haemoproteus*. *Plasmodium* spp. (not shown in Fig. 1)

TABLE 2. Prevalence of avian hematozoa and characteristics of the host community at 2-wk intervals during the year[a] in central Vermont, 1982–1985.

Interval	Number birds examined	Percent infected	Avian species	
			Present	Diversity[b]
1–15 Mar	67	25.4	10	2.485
16–31 Mar	24	40.0	8	2.755
1–15 Apr	135	17.0	14	3.084
16–30 Apr	311	42.1	18	3.011
1–15 May	174	56.9	20	3.481
16–31 May	196	56.1	27	3.731
1–15 Jun	71	73.2	15	3.301
16–30 Jun	69	73.9	14	3.807
1–15 Jul	19	78.9	9	2.614
16–31 Jul	39	69.2	15	3.273
1–15 Aug	57	59.6	18	3.685
16–31 Aug	6	50.0	2	0.918
1–15 Sep	25	56.0	8	2.173
16–30 Sep	20	20.0	5	1.291
1–15 Oct	43	20.9	9	3.169
16–31 Oct	39	25.6	7	2.348
1–15 Nov	23	26.1	4	1.413
16–31 Nov	22	13.6	6	1.933
1–15 Dec	65	23.1	8	2.442
16–31 Dec	14	28.6	4	1.727
1–15 Jan	30	13.3	3	0.674
16–31 Jan	9	22.2	3	1.530
1–15 Feb	5	40.0	1	0.000
16–28 Feb	79	20.3	5	2.026

[a] Data collected between March 1982 to March 1985 were pooled.
[b] The Shannon-Weiner Index of species diversity was used.

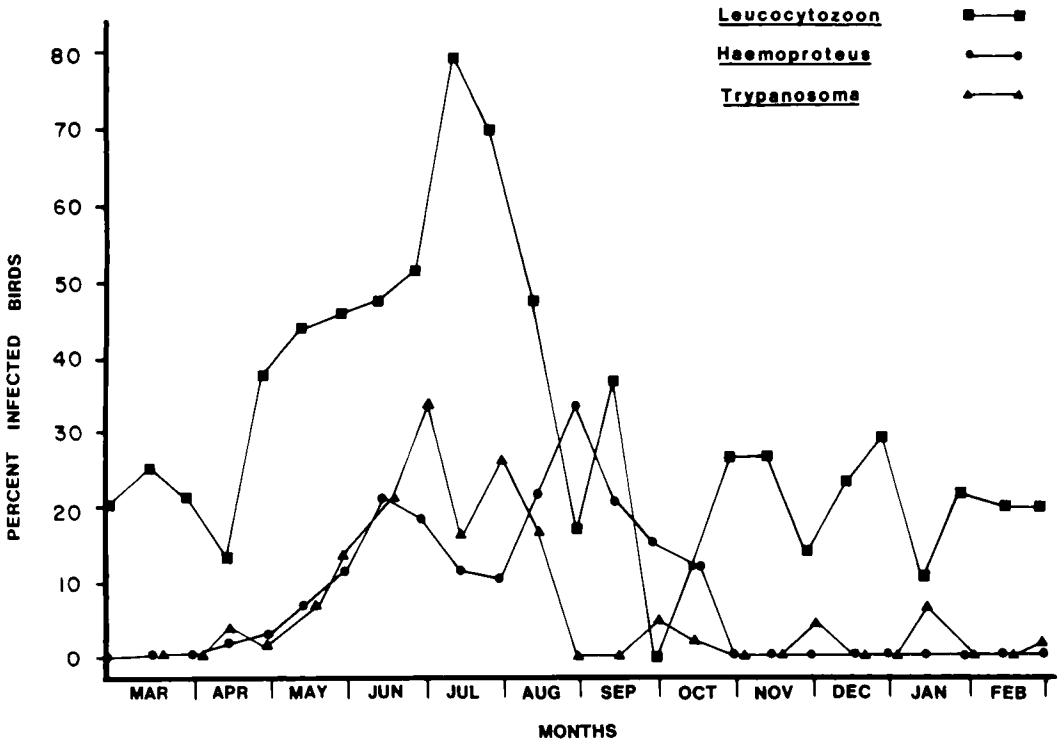

FIGURE 1. Seasonal prevalences of *Leucocytozoon* spp., *Haemoproteus* spp. and *Trypanosoma* spp. in birds in central Vermont from March 1982 to March 1985. Results for each half-month period in each of the 3 yr were summed.

were present in few birds in April and May. Most microfilariae were detected in birds examined in May and June.

The prevalences of hematozoa in mature and immature birds were compared. Chi-square analyses of data in Table 3 showed that immature birds had significantly higher prevalences of *Haemoproteus* and *Trypanosoma* than mature birds, but the prevalences of *Leucocytozoon* and *Plasmodium* did not differ between mature and immature birds. Microfilariae were not found in immature birds.

Birds examined during June, July and August were assumed to represent a sample of the breeding populations (summer residents) of the study area. Peak prevalences of *Leucocytozoon* and *Trypanosoma*, and high prevalence of *Haemoproteus* were detected in the breeding populations (Fig. 1). Prevalence of the protozoan genera in mature and immature summer residents showed no statistically significant differences (Table 4).

Birds examined in December, January and February represented a sample of the winter resident populations and nomadic species. Overall prevalence in these birds was 20.6% (*Leucocytozoon*—18.2%; *Trypanosoma*—1.8%; microfilariae—0.6%). No infections by *Haemoproteus* or *Plasmodium* were found (Table 5). When only winter residents that were also present during spring migration were considered (Table 6), the prevalence dropped from 28% in December to 12% in February. Statistically significant increases in prevalences of *Leucocytozoon*, *Haemoproteus* and *Trypanosoma* in these winter residents occurred during spring.

Intensities for *Trypanosoma* and microfilariae were almost always less than

TABLE 3. Prevalence of blood parasites in mature and immature birds in central Vermont, 1982–1985.

Age	Number examined	Number positive	Total infected with: L[a]	H	P	T	M
Mature	1,172	505	432	75[b]	3	55[c]	12
%		43.1	36.9	6.4	0.3	4.7	1.0
Immature	182	93	73	25	8	18	0
%		51.1	40.1	13.7	4.4	9.9	0

[a] Abbreviations: L = *Leucocytozoon* spp.; H = *Haemoproteus* spp.; P = *Plasmodium* spp.; T = *Trypanosoma* spp.; M = microfilariae.

[b] Prevalence in immature birds is significantly greater than in mature birds ($\chi^2 = 11.35$; $P < 0.001$).

[c] Prevalence in immature birds is significantly greater than in mature birds ($\chi^2 = 7.35$; $P < 0.01$).

one parasite/10,000 RBC. Haemoproteid infections ranged from less than one to 353 parasites/10,000 RBC, and intensities of infection by *Leucocytozoon* ranged from less than one to 54 gametocytes/10,000 RBC. Intensities of *Plasmodium* ranged from less than one to 225 infected cells/10,000 RBC. The mean intensity for *Leucocytozoon* spp. was 1.1 parasites/10,000 RBC (SD = 1.9), and highest average intensity (2.2 parasites/10,000 RBC) was seen in the last half of June. The mean intensity of infection by *Haemoproteus* spp. was 37.9 parasites/10,000 RBC (SD = 64.0), and the highest average intensity (83.4 parasites/10,000 RBC) was found in the last half of June.

DISCUSSION

In reviewing the literature on avian hematozoa of Region 5, Greiner et al. (1975) found about 39% of birds infected with blood parasites. The present study showed a comparable overall prevalence (42.5%), but the prevalence of specific hematozoa in central Vermont differed from that reported by Greiner et al. (1975). *Leucocytozoon* accounted for 22% of Region 5 avian infections while 36.5% of the birds in Vermont had parasites of this genus. *Haemoproteus* spp. were the second most commonly diagnosed blood parasites in Region 5 (18%), but were present in only 6.3% of birds in Vermont. *Trypanosoma* spp. were more prevalent (7.3%) in birds of the present study. Central Vermont birds were less commonly infected with *Plasmodium* (1.0%) compared to all of Region 5 birds (4%). These differences probably arose because the data of Greiner et al. (1975) on Region 5 contained information from coastal birds that tend to have low prevalences of hematozoans (Williams and Bennett, 1978), and because data on Region 5 included samples collected only during the spring or sum-

TABLE 4. Prevalence of avian hematozoa in mature and immature summer resident birds in central Vermont, 1982–1985.

Age	Number examined	Number positive	Total infected with: L[a]	H	P	T	M
Mature	159	114	96	28	1	41	5
%		71.7	60.4	17.6	0.6	25.8	3.1
Immature	81	58	50	13	2	16	0
%		71.6	61.7	16.1	2.5	19.8	0

[a] Abbreviations: L = *Leucocytozoon* spp.; H = *Haemoproteus* spp.; P = *Plasmodium* spp.; T = *Trypanosoma* spp.; M = microfilariae.

TABLE 5. Prevalence of avian hematozoa in winter residents (Dec–Feb) in central Vermont, 1982–1985. Bird species in which no parasites were found are listed separately, but are included in the totals.

	No. exam.	No. pos.	L*	T	M
Cyanocitta cristata	50	10	8	2	1
Coccothraustes vespertinus	23	3	3	0	0
Junco hyemalis	7	4	4	0	0
Spizella arborea	46	12	12	0	0
Totals	164	29	27	2	1
% of number examined		17.7	16.5	1.2	0.6

* Abbreviations: L = *Leucocytozoon* spp.; T = *Trypanosoma* spp.; M = microfilariae.

Negative species (sample size in parentheses): *Zenaida macroura* (1); *Columba livia* (3); *Parus atricapillus* (6); *Cardinalis cardinalis* (1); *Spizella pusilla* (1); *Carduelis tristis* (26).

mer when the prevalence is highest. Furthermore, Bennett and Cameron (1974) pointed out that the prevalence of avian hematozoa in an area is directly related to the area vector potential. Vector potential variation, no doubt, contributed to many of these differences.

Large differences in the prevalence of hematozoa among avian families are well known. Present results were similar to those reported for avian families in Region 5 (Greiner et al., 1975) and the mid-Atlantic area (Williams and Bennett, 1978). Hirundinidae, however, were infected more frequently in Vermont (35%) than in all of Region 5 (24%), or in New Jersey and Maryland (5%). Vermont Columbidae were infected less frequently (19%) than in all of Region 5 (63%). The differences among various families and within avian families of different regions probably resulted from the factors noted by Greiner et al. (1975). The factors include ecological differences, host susceptibility and behavioral variations, and sampling bias.

Bennett et al. (1974) pointed out the difficulties in interpreting data on prevalence of avian hematozoa that include information from migrating and resident birds. Bird banding records for the Northfield site kept since 1976 (Barnard, unpubl. data) showed that most spring migration took place between March and the first half of May. The breeding season extended from the second half of May through the end of August when fall migration began. The prevalences of hematozoa in the breeding population was high from June through August (Fig. 1, Table 4). Since no age-related differences in prevalences of protozoan hematozoa were found in summer residents (Table 4), the significant differences in overall prevalences of *Haemoproteus* spp. and *Trypanosoma* spp. in mature and immature birds (Table 3) probably resulted from contributions of migratory birds. The rea-

TABLE 6. Winter (Jan–Mar) and spring (Apr–May) prevalence of protozoan blood parasites in the resident birds regularly caught during the entire period (central Vermont, 1982–1985).

	Winter					Spring				
	No. exam.	No. pos.	L*	H	T	No. exam.	No. pos.	L	H	T
Spizella arborea	57	18	18	0	0	29	7	7	0	0
Carduelis tristis	46	0	0	0	0	59	18	9	0	11
Parus atricapillus	9	0	0	0	0	12	3	3	0	1
Cyanocitta cristata	44	8	7	0	2	35	27	18	12	17
Totals	156	26	25	0	2	135	55	37	12	29
% of birds examined		16.7	16.0	0	1.3		40.7	27.4	8.9	21.5

* Abbreviations: L = *Leucocytozoon* spp.; T = *Trypanosoma* spp.; H = *Haemoproteus* spp.

sons for these differences are obscure, but they might have resulted from age-related resistance mechanisms that caused more false negative diagnoses in mature birds than in immature birds. Alternatively, low species diversity (Table 2) in all but the breeding populations may have contributed to the differences if particularly susceptible species were disproportionately represented in the sample.

The prevalence of *Leucocytozoon* during April and May (Fig. 1) resulted from parasites in both resident and migrant birds. Potential vectors were probably not present at the study site in April and early May when prevalences rose abruptly. It was possible that mature birds encountered vectors during migration or in their southern wintering sites. Peak prevalence and intensity of *Leucocytozoon*, however, were recorded in breeding populations (Fig. 1). Relapse of *Leucocytozoon* infections took place in winter resident birds still present in the area during spring migration (Table 6). High prevalence subsequent to spring migration indicated that relapse occurred in the breeding populations (Fig. 1). The prevalence of *Leucocytozoon* in mature and immature birds of the breeding populations was not different, demonstrating that transmission occurred at a rapid rate. *Leucocytozoon* was consistently present in winter resident birds and, although intensities were low, no period of complete remission was seen.

An increase in the prevalence of *Haemoproteus* occurred during spring migration, but maximum prevalence was in birds of the breeding populations (Fig. 1). Maximum intensity of *Haemoproteus* infections (Fig. 1) preceded maximum prevalence in the breeding populations, suggesting that relapse was associated with both an increase in prevalence and intensity of infection. Prevalence of *Haemoproteus* in hatching-year birds was not significantly different from mature birds of the breeding populations (Table 4), demonstrating that transmission of *Haemoproteus* to hatching-year birds was efficient in the study area. Patent *Haemoproteus* infections were not demonstrated in winter residents, in contrast to infections by *Leucocytozoon* (Table 5), but relapse of infection was seen in some avian species that remained in the study area into early spring (Table 6).

An increase in prevalence of infections by *Trypanosoma* occurred during spring migration as it did in *Leucocytozoon* and *Haemoproteus*, but peak prevalence occurred in the breeding populations (Fig. 1). The peak prevalence of *Trypanosoma* spp. (33%) is remarkable. Direct microscopic examination of blood films is not the best method of detecting trypanosomes and the actual prevalence was probably higher (Bennett, 1962; Kirkpatrick and Lauer, 1985). As with *Leucocytozoon* and *Haemoproteus*, the prevalence of *Trypanosoma* in mature and immature birds of the breeding populations did not differ significantly. Transmission of *Trypanosoma* spp. in the study area occurred efficiently. Infections by *Trypanosoma* were evident in the winter resident populations, as with *Leucocytozoon*, but in contrast to *Haemoproteus* (Table 5). A spring relapse in prevalence of *Trypanosoma* was present in those species of winter resident birds that remained in the area during spring (Table 6).

The low prevalences of both *Plasmodium* and filariids prevent extensive discussion of their seasonal prevalences. The presence of *Plasmodium* spp. in immature birds of the breeding populations provided evidence that transmission took place in the study area (Table 4). The absence of microfilariae from immature birds (Table 3) may have resulted from the long prepatent periods characteristic of filariids (Bennett and Fallis, 1960) and does not rule out transmission in the area.

Conclusions drawn from this study were: (i) the overall prevalence of avian hematozoa in central Vermont was similar

to that reported for the whole of Region 5; (ii) while the prevalence of *Leucocytozoon* was about equal to that reported for Region 5, infections by *Haemoproteus* and *Plasmodium* were less prevalent, while those of *Trypanosoma* were more frequent; (iii) changes in the seasonal prevalence of hematozoa followed a well documented pattern, except that *Leucocytozoon* did not undergo a fall–winter period of remission as did *Haemoproteus*; (iv) peak intensity in *Leucocytozoon* spp. and *Haemoproteus* spp. preceded peak prevalence; and (v) transmission of protozoan hematozoa occurred in the study area.

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