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INTERSPECIFIC VARIABILITY OF PREVALENCE IN BLOOD PARASITES OF ADULT PASSERINE BIRDS DURING THE BREEDING SEASON IN ALASKA

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ABSTRACT: Blood parasite prevalence based on microscopic examination of stained blood smears was determined in adults of 11 passerine bird species sampled during their breeding season (May and June 1997–98) in interior Alaska (USA). These species included primarily Nearctic migratory species such as the dark-eyed junco (*Junco hyemalis*) and neotropical migratory species such as the blackpoll warbler (*Dendroica striata*), alder flycatcher (*Empidonax alnorum*), Swainson's thrush (*Catharus ustulatus*), northern waterthrush (*Seiurus noveboracensis*), and bank swallow (*Riparia riparia*) as well as one long-distance palearctic migrant, the arctic warbler (*Phylloscopus borealis*). The more prevalent parasites were *Leucocytozoon dubreuili* (73% of the sampled turdinids), *L. fringillinarum* (42% of the sampled fringillids and parulids), and *Trypanosoma avium* (39% of the sampled hosts). Other parasites (*H. fallisi:* 18% of the sampled turdinids; *Haemoproteus paruli:* 14% of the sampled parulids; *H. fringillae:* 5% of the sampled fringillids; microfilariae: 4% of the sampled hosts) were observed less frequently. *Plasmodium vaughani* was found only in two yellow warblers (*Dendroica petechia*). Overall parasite prevalence varied between 0% in the alder flycatcher to >80% in Swainson's thrush, arctic warbler, and Townsend's warbler (*Dendroica townsendi*). Prevalence of various hematozoa also was bird species-dependent. No relationship was observed between prevalence and either foraging (aerial versus trees/shrubs) or nesting habits (ground versus arboreal) or general location of the wintering area of the different species examined. Prevalence also was unrelated to average dates of arrival on breeding grounds and, therefore, to potential duration of exposure to local insect vectors before capture. Differences in blood parasite prevalence among species breeding in a same region and in the same type of habitat may result from differences in host specificity such as immunological resistance to infection or blood meal preference by potential vectors and/or in behavioral adjustments/physiological traits that alter exposure to vectors.

Key words: Blood parasites, boreal forest birds, dark-eyed junco, field study, *Haemoproteus paruli, Junco hyemalis, Leucocytozoon fringillinarum,* seasonal breeding, *Trypanosoma avium.*

INTRODUCTION

Interest in avian blood parasites has grown rapidly in recent years. This increase has to a large extent resulted from the hypothesis that parasites play a role in sexual selection (Hamilton and Zuk, 1982), and avian blood parasites have been repeatedly used to test this hypothesis (Møller, 1990; Zuk et al., 1990; Weatherhead and Bennett, 1992; Ratti et al., 1993). In addition, the traditional view that avian blood parasites are only slightly or not pathogenic has been challenged, as recent research has revealed important alterations in infected birds (Bennett et al., 1993; Nordling et al., 1998; Raidal and Jaensch, 2000). Finally, studies on avian blood parasites may be relevant to conservation issues (Dobson and McCallum, 1997).

Avian blood parasites are transmitted by blood-sucking arthropods including mosquitoes (Culicidae), biting midges (Ceratopogonidae), Louse Flies (Hippoboscidae), and Black Flies (Simuliidae) (Noble et al., 1989), and geographic differences and long-term changes in parasite prevalence presumably result partly from variations in parasite-specific vector abundance (Greiner et al., 1975; Bennett et al., 1982; Merilä et al., 1995). Factors other than local vector densities, however, also contribute to determining avian blood parasite prevalence. For example, this prevalence can vary intraspecifically as a func-

tion of age, sex, and season (Barnard and Bair, 1986; Gibson, 1990; Weatherhead and Bennett, 1991, 1992; Seutin, 1994; Norris et al., 1994). Seasonal variations partly result from alterations in host's susceptibility to infection that are associated with reproductive effort (Møller, 1990; Norris et al., 1994; Richner et al., 1994; Oppliger et al., 1996; Nordling et al., 1998). Interspecifically, it has been proposed that parasite prevalence is influenced by nesting and breeding habits (Greiner et al., 1975) as well as by average duration of incubation (Ricklefs, 1992). Finally, phylogenetically closely related species may have strikingly different parasite prevalences for reasons that are not currently understood (Forero et al., 1997).

To better understand the factors that account for interspecific differences in blood parasite prevalence, we determined the presence of haematozoa in eleven interior Alaska boreal forest-breeding passerines. To minimize the potentially confounding influences of age and sex, only adults and mostly males were sampled. In addition, all birds were caught in the same region and during their respective breeding season to attenuate potential effects of temporal or spatial factors or of reproductive condition on parasite prevalence. Species also were chosen that have similar incubation durations (11–16 days; Ehrlich et al., 1988), but differ with respect to their foraging and nesting (ground versus trees or shrubs) habits, allowing us to examine the proposed relationship between these habits and prevalence (Greiner et al., 1975).

Finally, we selected species that preferentially winter in a wide variety of regions including temperate North America such as the dark-eyed junco (*Junco hyemalis*; Ehrlich et al., 1988; Peterson, 1990), paleotropical areas such as the arctic warbler (*Phylloscopus borealis*, Cramp, 1992), and neotropical areas ranging from Mexico with species like the Lincoln's sparrow (*Melospiza lincolnii*) to South America with species such as the blackpoll warbler (*Dendroica striata*), alder flycatcher (*Empidonax alnorum*), Swainson's thrush (*Catharus ustulatus*), and bank swallow (*Riparia riparia*, Peterson, 1990; Curson et al., 1994). During the winter, species wintering in the tropics may be exposed to more and/or to a larger variety of insect vectors than species wintering in colder, more northern regions. Comparing tropical migrants with species that breed in the same regions, but remain at more northern latitudes during winter offers the opportunity to investigate the combined effects of breeding effort and of potentially prolonged exposure to high vector densities on parasite prevalence.

MATERIALS AND METHODS

Adult birds were caught during the breeding season from 24 May to 29 June 1997 (n = 83) and 1998 (n = 98). These included the alder flycatcher (n = 13), bank swallow (n = 18), Swainson's thrush (n = 11), Townsend's warbler (n = 10), blackpoll warbler (n = 13), yellow warbler (*Dendroica petechia*, n = 12), orange-crowned warbler (*Vermivora celata*, n = 15), arctic warbler (n = 6), northern waterthrush (*Seiurus noveboracensis*, n = 9), Lincoln's sparrow (n = 10), and dark-eyed junco (n = 64). All birds were caught in the vicinity of Fairbanks (Alaska, USA; 65°N; 148°W) except arctic warblers that were caught along the Denali Highway (Alaska; approximately 63°N; 146°W). Birds were collected using either Japanese mist nets and conspecific song taped playbacks or millet seed-baited Potter traps (some dark-eyed juncos only). Age and sex were determined based on plumage characteristics and on the presence of a developed cloacal protuberance (adult males) or incubation patch (adult females; Pyle 1997). The sample consisted only of males with the following exceptions: alder flycatchers [unknown (U) sex, n = 2], bank swallows [females (F), n = 10; U, n = 1], northern waterthrushes (F, n = 1; U, n = 1), and orange-crowned warblers (F, n = 3). Since blood parasites may show a diurnal periodicity (Gore et al., 1982), we caught most birds at approximately the same time of day (08:00 A.M. to 12:30 P.M. AST).

Within minutes of capture, we collected a blood sample from a brachial vein into a heparinized microhematocrit tube and we prepared a blood smear on a microscope slide according to Bennett (1970). Birds were then marked with a National Bird Survey (Laurel,

Maryland, USA) numbered aluminum leg band (permit number 22640) and they were released at the capture site. Slides were air-dried, labeled, fixed for 5 to 10 min in absolute methanol, stained using the Giemsa procedure (Bennett, 1970), cleared in 100% xylene, and cover-slipped using Cytoseal 60 (VWR Scientific Products, West Chester, Pennsylvania, USA).

Representative slides from the species under study were deposited at the U.S. National Parasite Collection (Beltsville, Maryland, USA; accession numbers 088310.00–088312.00, 088313.01, 088313.02, 088314.01–088314.04, 088315.00, 088317.01, 088317.02, 088318.00–088322.00, 088323.01, and 088323.02). To study smears, we examined each slide with a microscope at low (250×; 5 min) followed with high (400×; 10 min) magnification. Examination at low magnification resulted in survey of most of the smear, whereas during examination at high magnification at least 400 different fields were examined. All smears received the same overall search effort. Birds were classified as negative or positive for each parasite type. Prevalence was defined as the percentage of infected individuals in a sample.

Parasite species were identified by examining slides at 1,000× magnification under oil immersion. Microfilariae were not identified at the species level.

RESULTS

All trypanosomes were identified as *T. avium*, a widespread species that has been previously characterized and reported in several passeriforme families including Carduelinae, Passeridae, and Turdinae (Bennett et al., 1994a). Infections of *Leucocytozoon* spp. were of *L. fringillinarum* except those in Swainson's thrushes which were *L. dubreuili*. Infections of *Haemoproteus* spp. were of *H. fallisi* in Swainson's thrushes, *H. paruli* in the four warbler species, and *H. fringillae* in Lincoln's sparrows and dark-eyed juncos. *Plasmodium vaughani* was observed in samples from two yellow warblers (for terminology, see Bennett and Peirce, 1988; Burrey-Caines and Bennett, 1992; Bennett et al., 1994b). The prevalence of parasites in the samples obtained from each species is summarized in Table 1.

Combining all host species, 60% of the samples were infected with parasites. The most prevalent parasites were *T. avium* (39% of the sampled hosts) and *Leucocytozoon* (*L. dubreuili:* 73% of the sampled turdinids; *L. fringillinarum:* 42% of the sampled fringillids and parulids). *Haemoproteus* spp. and microfilariae were detected in a relatively small proportion of the sampled birds (*H. fallisi:* 18% of the sampled turdinids; *H. paruli:* 14% of the sampled parulids; *H. fringillae:* 5% of the sampled fringillids; microfilariae: 4% of the hosts).

Overall parasite prevalence was species-specific, varying from 0% in the alder flycatcher to 90% in the Townsend's warbler. Similar differences were observed for individual parasite species. For example, *L. fringillinarum* was not detected in alder flycatchers and bank swallows, but was present in 59% of the samples collected from dark-eyed juncos. Likewise, *T. avium* was not detected in alder flycatchers, but was present in 70% of the samples collected from Townsend's warblers. Further, *Haemoproteus* sp. was altogether absent from samples collected from four host species, but *H. paruli* was present in 42% of the samples collected from yellow warblers. Finally, the highest prevalence of the common parasites was found in different host species (*L. dubreuili* in Swainson's Thrush, *T. avium* in Townsend's warbler, and *H. paruli* in yellow warbler).

Prevalence of parasites was not consistently associated with foraging habits. For example, prevalence of *T. avium* and *L. fringillinarum* differed markedly between alder flycatchers, bank swallows, Townsend's warblers, arctic warblers, and yellow warblers, all of which are primarily arboreal/aerial foragers. As a group, predominantly ground nesters (arctic and orange-crowned warblers, northern waterthrush, dark-eyed junco, and Lincoln's sparrow) had similar *T. avium* and *L. fringillinarum* prevalences as shrub/tree nesters (alder flycatcher; blackpoll, Townsend's, and yellow warblers; Swainson's thrush).

We found no evidence that parasite prevalence was associated with distance traveled between breeding and putative

TABLE 1. Blood parasite prevalence in migratory songbirds caught on their breeding grounds in interior Alaska (USA).

Species	Capture dates	Median date	Parasites					
			Leucocytozoon	*Trypanosoma*	*Haemoproteus*	Microfilariae	*Plasmodium*	Total
Empidonax alnorum, (*n* = 13)	5/28–6/17	6/9	0	0	0	0	0	0
Riparia riparia, (*n* = 18)	6/1–6/3	6/1	0	11[c]	0	0	0	11
Catharus ustulatus, (*n* = 11)	5/24–6/28	5/31	73[a]	55[c]	18[d]	27	0	82
Dendroica townsendi, (*n* = 10)	5/26–6/28	6/28	30[b]	70[c]	10[e]	0	0	90
Dendroica striata, (*n* = 13)	5/24–6/25	5/31	39[b]	23[c]	8[e]	0	0	54
Dendroica petechia, (*n* = 12)	5/24–6/26	5/30	8[b]	25[c]	42[e]	0	17[g]	67
Vermivora celata, (*n* = 15)	5/24–6/18	5/30	27[b]	27[c]	0	0	0	53
Phylloscopus borealis, (*n* = 6)	6/17–6/17	6/17	17[b]	67[c]	0	0	0	83
Seiurus noveboracensis, (*n* = 9)	5/24–6/26	6/21	33[b]	56[c]	22[e]	0	0	78
Melospiza lincolnii, (*n* = 10)	5/27–6/13	5/29	30[b]	30[c]	10[f]	10	0	60
Junco hyemalis, (*n* = 64)	5/29–6/29	6/20	59[b]	52[c]	5[f]	6	0	75
Overall prevalence across all species:			37	39	9	4	1	60

[a] = *Leucocytozoon dubreuili.*
[b] = *Leucocytozoon fringillinarum.*
[c] = *Trypanosoma avium.*
[d] = *Haemoproteus fallisi.*
[e] = *Haemoproteus paruli.*
[f] = *Haemoproteus fringillae.*
[g] = *Plasmodium vaughani.*
For each species, the table indicates the sample size (in parenthesis) and inclusive as well as median capture dates.

wintering grounds. For example, this prevalence was similar in the dark-eyed junco, a predominantly North American migrant, and in a considerably longer-distance migrant, the Swainson's thrush. Further, prevalence differed markedly across species of long-distance migrants that winter in tropical regions (bank swallow; alder flycatcher; blackpoll, yellow, and arctic warblers).

DISCUSSION

Overall prevalence (60%) of blood parasites in interior Alaska passerines was similar to or higher than that reported in passerines sampled in other middle and high latitude regions such as Labrador (Bennett, 1972), Vermont (Barnard and Bair, 1986), Ontario (Weatherhead and Bennett, 1991, 1992), and Finland (Merilä et al., 1995). In particular, the average prevalence of *Trypanosoma avium* infection in the present investigation was 39% whereas in other studies *Trypanosoma* sp. was <10% (Weatherhead and Bennett, 1992; Merilä et al., 1995), 7% (Barnard and Bair, 1986), 4% (Greiner et al., 1975), and <1% (Bennett et al., 1982) of the sampled birds. Studies comparing parasite prevalence either in one avian species across its geographical range (Merilä et al., 1995) or in several species across years (Bennett et al., 1982) suggest that this prevalence declines following human-related natural habitat degradation. Our study region (interior Alaska boreal forest) has undergone minimal human influence and has a high density of dipteran vectors during the breeding season (Gjullin et al., 1961). It may, therefore, host particularly high densities of *T. avium* vectors, accounting for the high prevalence of this species. Alternately, the host species that we examined may altogether be particularly susceptible to infection by *T. avium*. Finally, the relatively high prevalence may have resulted from these birds being caught during the breeding season, when parasite prevalence is generally higher than at other times (Weatherhead and Bennett, 1991, 1992; Young et al., 1993; see below).

In the present as well as in previous investigations (Bennett and Fallis, 1960; Greiner et al., 1975; Young et al., 1993), there were large interspecific differences in overall parasite prevalence. For example, we found no parasites in alder flycatchers and only 11% of the sampled barn swallows were parasitized, but hematozoa were detected in over 70% of the samples collected from several other species. These observations apply to individual parasite species as well (see Table 1) and raise the question of what factors regulate interspecific variations in prevalence.

Within a given species, prevalence can vary spatially (greenfinch, *Carduelis chloris*, Merilä et al., 1995) and, in a given area, also seasonally (Bennett et al., 1982; Weatherhead and Bennett, 1992). All the birds used in this study were caught in the same region and at the same time of year, suggesting that interspecific differences in prevalence did not result from proximate spatial or temporal influences. In some bird species, the same parasite types infect males and females, but the prevalence of specific parasites is sex-dependent and lower in yearlings than adults (Weatherhead and Bennett, 1991, 1992; Merilä et al., 1995). Age- and sex-related effects on prevalence are unlikely to account for the differences observed in this study, however, because we sampled only adults and most birds were males. Based on an extensive survey of the literature pertaining to the prevalence of hematozoa in North America, Greiner et al., (1975) proposed that in a given geographical area, this prevalence is highest in birds nesting in the mid-canopy of forest environments. Our results, albeit limited to a smaller number of species than in Greiner et al. (1975) study, do not support the hypothesis that nest location and parasite prevalence are related. Indeed, prevalence did not differ consistently between preferentially ground-nesters (arctic and orange-crowned warblers, northern waterthrush,

dark-eyed junco, and Lincoln's sparrow) or a cavity-nester (bank swallow) and the remaining species, all of which preferentially nest in trees and/or shrubs.

There is evidence that several weeks separate the inoculation of blood parasites by insect vectors from the appearance of these parasites in the bird circulation (Desser and Bennett, 1993). The bird species examined in this study typically reach their northern breeding grounds at different times, varying from the end of April–early May (dark-eyed junco) to end of May and the first half of June (e.g., alder flycatcher, Swainson's thrush, arctic warbler). At the time of sampling, late-arriving species had, therefore, possibly been exposed to local vectors for a shorter period than early-arriving species. Prevalence was, however, as high in an early (dark-eyed junco) as in a late (Swainson's thrush) migrant and it differed markedly among late-arriving species (Swainson's thrush, alder flycatcher, arctic warbler). Thus, average dates of arrival on breeding grounds were apparently not related to prevalence.

Hematozoa have been found in many birds living in the Neotropics (Sousa and Herman, 1982; Bennett et al., 1991; Young et al., 1993), but at least in some cases (*Leucocytozoon* sp.) prevalence was considerably less in these birds than in those inhabiting nearctic regions (White et al., 1978). Furthermore, a study of passerine birds in Newfoundland (Bennett et al., 1974) led to suggest that transmission of hematozoa takes place in the breeding areas rather than during migration or on wintering grounds. Accordingly, birds wintering at low latitudes, but breeding in other regions, are unlikely to become infected outside the reproductive period. The present results are consistent with this proposition. The exact wintering areas of the host populations that we sampled are not identified, but it is known that the studied species preferentially winter across a broad range of latitudes in the USA (dark-eyed junco), in tropical South America (Swainson's thrush, blackpoll warbler, alder flycatcher, northern waterthrush, bank swallow), and in tropical Asia (arctic warbler). We found no (or very low) hematozoan prevalence in two neotropical migrants (alder flycatcher and bank swallow), but blood parasites were present in over 50% of other tropical migrants (blackpoll and arctic warblers, northern waterthrush, Swainson's thrush). Further, prevalence was equally high in dark-eyed juncos and Swainson's thrushes. Thus, specific differences between latitude of breeding and putative wintering grounds were apparently not related to prevalence. Similarly, no difference in prevalence was detected between migratory and sedentary European birds (Kucera, 1983).

Absence of relationship between latitude of overwintering and parasite prevalence may relate to the fact that susceptibility to parasite infection depends on the host's physiological condition. Several studies have found that reproductive effort decreases parasite resistance (Møller, 1990; Norris et al., 1994; Richner et al., 1994; Oppliger et al., 1996; Nordling et al., 1998). Irrespective of vector densities, likelihood of successful infection is, therefore, presumably lower outside than during the reproductive period (Bennett et al., 1974). In rodents, changes in host immunity following infection may result in rapid destruction of some parasites (*Trypanosoma lewisi:* Giannini and D'Alessandro, 1984). Similar changes may operate in migratory birds, resulting in suppression or even elimination of infections acquired on wintering grounds prior to these birds reaching summer breeding areas.

In conclusion, the present investigation demonstrates that adult passerines sampled during the breeding season and in a same boreal forest region exhibit large specific differences in hematozoan prevalence. We found no evidence that these differences correlate with age, breeding habitat, reproductive status, nesting or foraging habits, time of arrival on breeding grounds, or distance traveled between breeding and wintering regions. As re-

cently suggested (Forero et al., 1997), species-specific physiological (immunological) factors acting either prior to and/or during the breeding season probably account for specific differences in parasite prevalence during this season. Species occupying a same breeding habitat may also have evolved specific behavioral adjustments that allow them to minimize their exposure to vectors independent of their physiological susceptibility to these vectors.

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