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HEMOSPORID PARASITE COMMUNITIES OF WATERFOWL (ANATIDAE) FROM THE KELLOGG BIOLOGICAL STATION AND DOUGLAS LAKE, MICHIGAN

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RANDALL J. DEJONG

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Patrick M. Muzzall
Major professor

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HEMOSPORID PARASITE COMMUNITIES OF WATERFOWL (ANATIDAE) FROM THE KELLOGG BIOLOGICAL STATION AND DOUGLAS LAKE, MICHIGAN

By

Randall John DeJong

A THESIS

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ABSTRACT

HEMOSPORID PARASITE COMMUNITIES OF WATERFOWL (ANATIDAE) FROM THE KELLOGG BIOLOGICAL STATION AND DOUGLAS LAKE, MICHIGAN

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Totals of 218 and 114 wild waterfowl from the Kellogg Biological Station (KBS) area in southwestern Michigan were examined for hematozoan parasites in summer and fall 1995, respectively. Fifty-five common mergansers were examined from Douglas Lake in northern lower Michigan in July 1995. *Haemoproteus nettionis, H. greineri*, and *Leucocytozoon simondi* occurred in KBS waterfowl, with *H. nettionis* the most common. *Haemoproteus greineri* and *L. simondi* frequently and *Plasmodium circumflexum* infrequently infected Douglas Lake common mergansers. Overall hematozoan prevalence was higher in the fall than the summer in KBS waterfowl and was much higher in Douglas Lake common mergansers than both summer and fall KBS waterfowl. Intensity of *H. nettionis* in KBS waterfowl was lower in the fall. Transmission of hemosporids did not occur at KBS and the abundance of potential vectors appeared low. In contrast, high transmission was evident at Douglas Lake and appeared to be responsible for differences in component communities between the two locations. The component communities in KBS waterfowl were isolationist in character while those at Douglas Lake demonstrated some evidence of species interactions. Common merganser is reported as a new host record for *H. greineri* and *P. circumflexum.*

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INTRODUCTION

The structure and organization of parasite communities can be highly complex and are the product of long and continuing interactions involving both host and parasite populations over evolutionary time (Esch et al., 1990). In ecological time, the structure and organization of parasite communities can be influenced quickly by certain factors. One such factor that can influence community structure is transmission rate; very different community structures are thought to be produced by low and high transmission rates. Low transmission rates should produce communities that are unsaturated and in nonequilibrium and that provide few opportunities for interspecific interactions. Such a community can be characterized as isolationist (Holmes and Price, 1986). On the other hand, high transmission rates should lead to saturation and equilibrium, providing more opportunities for interspecific interactions. Such a community would be characterized as interactive (Holmes and Price, 1986).

Transmission itself is dependent upon other factors. These can be broadly divided into abiotic and biotic factors (Holmes and Price, 1986). Abiotic factors include temperature, humidity, etc. Biotic factors can be divided into host-intrinsic factors, such as host species, age, sex, and immune response, and parasite-intrinsic factors, such as parasite species, development rate, and reproductive rate.

Parasite communities are naturally hierarchical. The parasites of individual hosts, termed infracommunities, collectively comprise all of the parasites in all individuals of a given host species within an ecosystem, termed the component community (Holmes and Price, 1986). Likewise, parasite populations are hierarchical and form the basis for the community hierarchy. Infrapopulations refer to the population of a single parasite species within an individual host which collectively form the infracommunity. Metapopulations

are all members of a parasite species which infect a given host species within an ecosystem. Collectively, metapopulations form component communities.

Of the many component communities of birds (intestinal helminths, intestinal protozoa, ectoparasites, among others), only the hematozoan community uses the bloodstream for growth and reproduction. Hematozoan communities can include intracellular hemosporids (Apicomplexa, Hemosporina, Plasmodiidae), filarial nematodes (Nematoda, Filaroidea, Onchocercidae), and trypanosomes (Sacrcomastigophora, Kinetoplastida). All utilize hematophagous arthropods as vectors. Hemosporid parasites of birds, i.e., species of *Haemoproteus, Leucocytozoon,* and *Plasmodium* have received much attention by parasitologists and ornithologists worldwide. Hemosporids can be ecologically important, such as in their role in the decline of native birds in Hawaii (van Riper III et al., 1986). They are also probably evolutionarily important in birds, and recently investigators have studied their possible role in the evolution and maintenance of sexual dichromaticism and dimorphism in birds (the Hamilton-Zuk hypothesis--Hamilton and Zuk, 1982; see review by Clayton, 1991). Filarial nematodes and trypanosomes are reported less often and their importance is less understood.

Ducks, geese, and swans (Anseriformes: Anatidae) are important because domesticated species are used for food and wild species for recreational bird watching and hunting. Consequently, the parasites of the Anseriformes have been studied more than the parasites of any other group of birds except the Galliformes.

The term waterfowl usually applies only to the Anatidae, and not to all aquatic birds. I follow this convention and use the term waterfowl to refer to the Anatidae only. Hemosporids are among the most studied of waterfowl parasites (Bennett and Squires-Parsons, 1992). *Leucocytozoon simondi,* the only species of *Leucocytozoon* that occurs in anatids, causes high mortality in domestic flocks of waterfowl (O'Roke, 1934; Fallis et al., 1951; Chernin 1956a). *Leucocytozoon simondi* also can cause mortality in wild populations. O'Roke (1934) reported losses in wild mallards (*Anas platyrhynchos*) and

black ducks (*A. rubripes*) in northern Michigan. Herman et al. (1975) cited the parasite as a limiting factor of the Canada goose (*Branta canadensis*) population at the Seney National Wildlife Refuge in the upper peninsula of Michigan. Of limited or no known pathogenicity in waterfowl are *Plasmodium* spp. (see Greiner et al., 1975b; Wobeser, 1981), with 11 species in anatids (Bennett et al., 1993). Waterfowl species of *Haemoproteus, H. nettionis* and *H. greineri*, are also of limited or no known pathogenicity (see Wobeser, 1981; Bennett et al., 1984). *Trypanosoma* spp. are not known to cause disease in waterfowl (Herman, 1968; Wobeser, 1981) and the pathogenicity of filarial nematodes in waterfowl is controversial (Wobeser, 1981).

Host specificity of hemosporids varies between genera. *Haemoproteus* has been proven to be family specific (Atkinson, 1986), meaning that *H. nettionis* and *H. greineri* only infect species of Anatidae. *Leucocytozoon* spp. are also believed to be family specific, based on morphology and vectors (Bennett et al., 1994); *Leucocytozoon simondi* only infects species of Anatidae. *Plasmodium* spp., however, are not completely family-specific and some species infect more than one bird family (Bennett et al., 1993).

The life cycles of hemosporid genera are similar (Figure 1). All three genera utilize female true flies (Diptera) as vectors. *Haemoproteus, Leucocytozoon,* and *Plasmodium* use biting midges (Ceratopogonidae) and hippoboscid flies (Hippoboscidae), black flies (Simuliidae), and mosquitoes (Culicidae), respectively. Vectors of *Haemoproteus* spp. in waterfowl are believed to be ornithophilic *Culicoides* spp. throughout the world, based on the determination of *C. downesi* as a vector of *H. nettionis* in eastern North America (Fallis and Wood, 1957). Sibley and Werner (1984) reported *C. downesi* as a vector of *H. nettionis* in Michigan's upper peninsula. The vectors of *H. greineri* are presumed to be *Culicoides* spp. as well. Vectors of *Leucocytozoon simondi* are several species of ornithophilic *Simulium* (see O'Roke, 1934). Vectors of *Plasmodium* spp. of waterfowl are *Culex* spp. and *Culiseta* spp. (see Meyer and Bennett, 1976; Work et al., 1990).

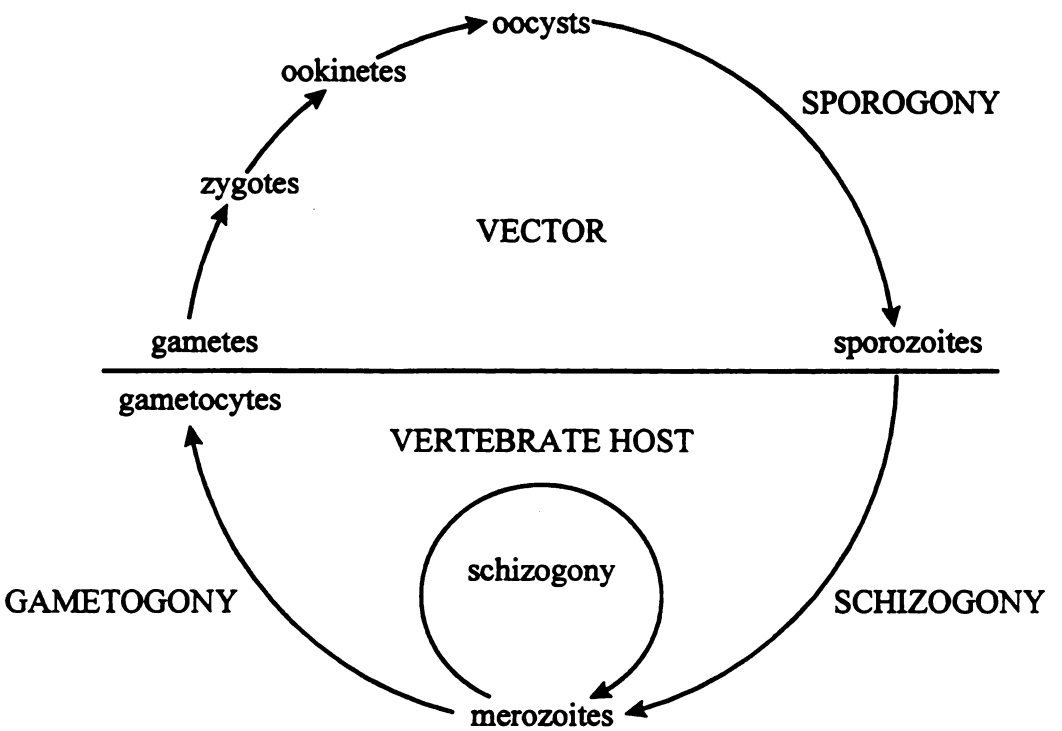

Figure 1. Diagram of the hemosporid life cycle. Redrawn from Atkinson and van Riper III (1991).

Transmission to waterfowl occurs when the vector injects sporozoites into the bird while obtaining a blood meal. Sporozoites invade host tissues such as the liver, grow, and reproduce asexually (schizogony) to produce merozoites.

Although the life cycles of *Haemoproteus, Leucocytozoon,* and *Plasmodium* are similar, they differ in the types of tissue where schizogony occurs. *Haemoproteus* and *Leucocytozoon* undergo schizogony in fixed, non-circulating cells only, and the only stages of development in circulating blood cells are gametocytes. In the case of *Plasmodium,* schizogony occurs in the fixed non-circulating cells as well as in circulating erythrocytes; therefore both gametocytes and schizonts may be found in blood cells. The presence of both gametocytes and schizonts is a key difference that separates *Plasmodium* from the other two genera (Greiner and Bennett, 1975, Greiner et al., 1975b, Atkinson and van Riper III, 1991).

Merozoites can reinvade liver cells or invade circulating blood cells. In the case of *Leucocytozoon*, some merozoites invade leukocytes and some invade erythrocytes, whereas *Haemoproteus* and *Plasmodium* merozoites invade only erythrocytes. Upon invading blood cells, merozoites develop into gametocytes (gametogony).

When another suitable vector ingests gametocytes, the life cycle is continued. In the midgut of the vector, sexual reproduction occurs when gametes form from the gametocytes (gametogenesis) and then fuse to form zygotes. Zygotes transform into elongate ookinetes which penetrate the insect's midgut epithelium and develop into oocysts within cells. Asexual reproduction (sporogony) occurs in the oocyst to yield numerous infective sporozoites. These rupture the epithelial cell and move to the salivary glands where they remain until the vector's next blood meal (Atkinson and van Riper III, 1991).

The duration of each hemosporid life stage varies between genera and species; only estimates are known for some. Of particular importance to the present study, however, is the length of time required for the waterfowl host to develop a parasitemia

(circulating gametocytes) after the infective bite of a vector, termed the prepatent period. For *H. nettionis*, the prepatent period in waterfowl is approximately 14 days (Fallis and Wood, 1957). The prepatent period of *H. greineri* is not known, but is presumed to be similar to *H. nettionis*. For *L. simondi*, the prepatent period is 7-9 days (Kocan and Clark, 1966a; Desser and Ryckman, 1976). *Plasmodium* spp. have a prepatency period of 14-19 days in ducks and 31 days in geese (Meyer et al., 1974).

In temperate climates, transmission of hemosporids primarily occurs in the spring and early summer, during the breeding season of birds and emergence period of vectors. Adult birds with chronic infections suffer a seasonal increase in parasitemia, or spring relapse, that coincides with egg-laying in female birds (Chernin 1956b) increasing the likelihood that newly hatched vectors will obtain parasites. The number of bird hosts is increased when infected vectors obtain subsequent blood meals from hatchlings and sporozoites are injected (Atkinson and van Riper III, 1991).

Surveys of wild waterfowl in Michigan have been few and limited to the northern lower peninsula and the upper peninsula (O'Roke, 1931, 1934; Herman et al., 1975). In addition, several experimental and transmission studies of waterfowl hematozoa were completed at Douglas Lake in the northern lower peninsula (O'Roke, 1931, 1934; Chernin, 1956a; Barrow et al., 1968) and at various locations in the upper peninsula (Tarshis, 1976; Desser et al., 1978; Sibley and Werner, 1984). Work has not been done on waterfowl hematozoa in southern Michigan, except for a report by Kocan (1966) of a canvasback (*Aythya valisineria*) infected with a *Plasmodium* sp. captured at the Kellogg Biological Station in southwestern Michigan. He believed that the canvasback was migrating (it was captured in November) and had acquired its infection on its breeding grounds.

The terms and concepts for parasite communities developed by Holmes and Price (1986), Esch et al. (1990), and others are based on helminth communities, but can be applied to hematozoan communities. Yet only a few investigators have done so. Godfrey

et al. (1990) examined the effects of host-intrinsic factors and collection location on the haemoproteid community (*Haemoproteus* spp. only) of mourning doves in western Texas. Fedynich and Rhodes, Jr. (1995) analyzed the structure and pattern of the hematozoan community of wintering turkeys in South Carolina. Fedynich et al. (1993) studied the structure and pattern of the hematozoan community of three species of waterfowl wintering in south Texas.

The objectives of this study were to characterize the hematozoan community of waterfowl from the Kellogg Biological Station area in southwestern Michigan by 1) evaluating the effects of host-intrinsic factors, such as species, age, and sex, 2) evaluating the effects of season, 3) monitoring transmission in the KBS area, and 4) identifying vectors which might have a role in transmission. In addition, common mergansers (*Mergus merganser*) from Douglas Lake in northern lower Michigan were examined for blood parasites. The effects of host-intrinsic factors were evaluated in common merganser data. Comparisons of hematozoan communities are made between the two locations.

MATERIALS AND METHODS

Descriptions of Hemosporids

The most diagnostic characters for hemosporids are gametocyte shape and color, position of the host cell nucleus, and the number of pigment granules in the parasite cytoplasm. Also, the character of any red bodies is used in distinguishing between *Haemoproteus* spp. gametocytes and *Plasmodium* spp. schizonts.

Haemoproteus nettionis Johnston and Clelland, 1910 is nearly global in distribution, presumably throughout the range of the Anatidae, and has been reported from at least 47 waterfowl species (Williams and Bennett, 1980). The macrogametocytes are robustly halteridial, or crescent-shaped with a smooth margin. The host cell nucleus is laterally displaced, sometimes completely to the periphery. The parasite cytoplasm stains blue with Giemsa's stain. Pigment granules are present in the cytoplasm, usually discrete and yellow-brown in color and average 24 granules per parasite. Numerous volutin granules, staining pink-red in color, are sometimes present (E. C. Greiner, *pers. comm.*). The parasite nucleus stains pink to rose in color and occupies approximately 5% of the parasite area. The parasite occupies approximately 80% of the erythrocyte-parasite complex, hypertrophying the host cell (25%) and atrophying the host cell nucleus (18%) in area. The microgametocytes are similar in appearance to the macrogametocyte, but displace the host cell nucleus slightly more and the parasite cytoplasm stains a lighter blue with Giemsa's stain (Williams and Bennett, 1980; Bennett and Pierce, 1988).

Haemoproteus greineri Bennett, Turner, and Whiteway, 1984 has been reported from at least seven waterfowl species and is considered endemic to the prairie provinces of Canada (Bennett et. al., 1984; Fedynich et. al., 1993). The macrogametocytes are circumnuclear, meaning that they completely encircle the erythrocyte nucleus. The

margin of the parasite is entire, not ameboid. The host cell nucleus is usually slightly laterally displaced or not at all, although it is rarely displaced to the periphery. The parasite cytoplasm stains a deep blue with Giemsa's stain. Yellow-brown pigment granules are present, but are smaller and more numerous (averaging 38 per parasite) than for *H. nettionis*. Numerous volutin granules, staining pink-red in color, are sometimes present (E. C. Greiner, *pers. comm.*). The parasite nucleus stains deep pink with Giemsa's stain and averages about 9% of the parasite area. The parasite occupies 90% of the erythrocyte-parasite complex, hypertrophying the host cell (20%) and atrophying the host nucleus (14.5%) in area. There are also "round" forms of the macrogametocyte that show gross hypertrophy in width of the parasitized erythrocyte. The microgametocyte is similar in appearance to the macrogametocyte, but averages slightly fewer pigment granules (35), stains a lighter blue with Giemsa's stain, and possesses a nucleus which constitutes a larger portion (41%) of the parasite area (Bennett et al., 1984; Bennett and Pierce, 1988).

Leucocytozoon simondi Mathis and Leger, 1910 has a well documented distribution, especially in North America, and is considered a parasite of Holarctic anatids. It has been reported from at least 42 waterfowl species (Bennett and Squires-Parsons, 1992). The macrogametocytes occur in both round and fusiform morphs. The round morph is round to broadly ovoid, but prone to be distorted into a variety of shapes. The parasite occupies 80-85% of the area of the host cell-parasite complex. The parasite cytoplasm stains blue with Giemsa's stain and no pigment granules are present. The parasite nucleus stains pink with Giemsa's stain and is round to broadly ovoid, occasionally narrowly elliptical, and occupies 7% of the area of the parasite. The nucleus of the host cell is displaced, forming a distinct cap on the host-parasite complex and covering 33% of the periphery of the parasite and 16% of the area of the host cell-parasite complex.

The fusiform morph of the *L. simondi* macrogametocyte occupies only 65% of the host cell-parasite complex, is narrowly ovoid to elliptical in shape, and is never round. The parasite cytoplasm and nucleus stain similarly to that of the round morph and again no pigment granules are present. The nucleus of the host cell lies along one side as a narrow ribbon, and expands into two terminal bulbs. The host nucleus covers 45% of the periphery of the parasite and occupies 30% of the area of the host cell-parasite complex (Bennett and Squires-Parsons, 1992).

The microgametocyte also occurs in both round and fusiform morphs. The round microgametocyte has similar measurements to round macrogametocytes, but the fusiform microgametocyte averages 5-10% smaller than the fusiform macrogametocyte. Both morphs of the microgametocyte stain lighter in color with Giemsa's stain (Bennett and Squires-Parsons, 1992).

Plasmodium circumflexum Kikuth, 1931 has been described from 43 avian families and 138 species and is global in distribution (Bennett et al., 1993). The macrogametocytes are nearly circumnuclear with an irregular margin. The host cell nucleus is usually laterally displaced. The parasite cytoplasm stains blue with Giemsa's stain. Brown pigment granules are numerous and scattered. The microgametocyte is similar to the macrogametocyte, but stains red in Giemsa's (Garnham, 1966).

As stated above, *Plasmodium* spp. differ from *Haemoproteus* spp. and *Leucocytozoon* spp. in having intraerythrocytic schizogony. Mature erythrocytic schizonts of *P. circumflexum* are circumnuclear, do not displace the host cell nucleus, and the merozoite nuclei can resemble volutin granules, making them very similar in appearance to *H. greineri* gametocytes. However, the schizont nuclei are often larger, are less round, possess a 'halo' around them, and are never immediately adjacent to one another (*pers. observ.*). The number of merozoites present in a mature schizont ranges from six to thirty (Garnham, 1966; Greiner et al., 1975b; E. C. Greiner, *pers. comm.*).

Descriptions of Study Locations

The Kellogg Biological Station Area

The W.K. Kellogg Biological Station (KBS) of Michigan State University lies in southwestern Michigan, at 42°24'N, 85°24'W. This study focused on three locations within or adjacent to the station: Gull Lake, the Kellogg Bird Sanctuary, and the Kellogg Farm (Figure 2).

Gull Lake. Gull Lake is an alkaline, oligotrophic to mesotrophic lake approximately 822 ha in surface area and up to 35 m deep. The entire lakeshore is developed and heavily populated, and the lake is extensively used for recreation and fishing. Mallards are the only waterfowl species to breed on this lake, although other species use it during the migratory seasons. Typically, about 12 broods of mallard ducklings are produced each year (W. C. Johnson, *pers. comm.*).

Kellogg Bird Sanctuary. The Kellogg Bird Sanctuary totals 25 ha in area and its most prominent natural feature is Wintergreen Lake. Wintergreen Lake is small (15 ha), shallow (6.3 m maximum depth), and alkaline. Resident and migratory waterfowl populations contribute substantial nutrient input and the lake is considered hypereutrophic. Approximately 3-5 wood duck (*Aix sponsa*), 5-8 mallard, and 10-12 Canada geese broods are produced on Wintergreen Lake each year. Including these broods, about 50 wood ducks, 200 mallards, and 100 Canada geese use this lake during the summer. During the migratory season, the lake is used by over 3000 Canada geese, 2000 wood ducks, mallards, and other duck species, and by 50-100 swan. Over the last 20 years, the number of ducks, geese, and swan using the lake has remained constant (W. C. Johnson, *pers. comm.*). Wintergreen Lake is approximately 300 m from the shore of Gull Lake and approximately 1500 m away from the biological laboratories of KBS. Other habitats of Kellogg Bird Sanctuary include smaller ponds used for captive waterfowl near Wintergreen Lake, and mature beech-maple forest.

Figure 2. The Kellogg Biological Station (KBS) area in southwestern Michigan and Douglas Lake in northern lower Michigan. The KBS area includes Gull Lake, Wintergreen Lake, and Kellogg Farm. (Figure redrawn based on Tiger Mapping Service, U.S. Census Bureau).

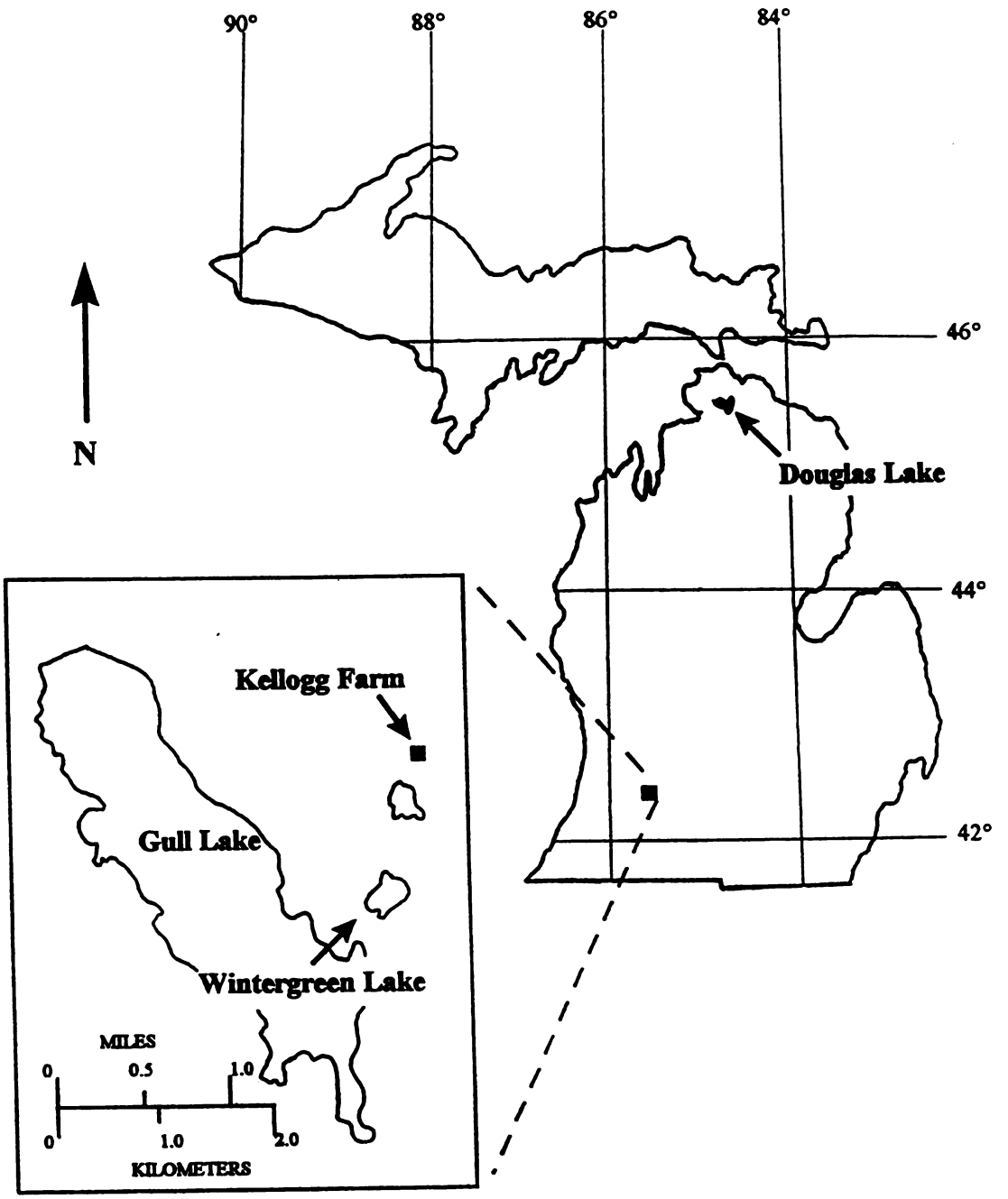
90°
88°
86°
84°
46°
44°
42°
N
Douglas Lake
Kellogg Farm
Gull Lake
Wintergreen Lake
MILES
0
0.5
1.0
0
1.0
2.0
KILOMETERS

Figure 2.

Kellogg Farm. The Kellogg Farm is a dairy farm dedicated to research and education. The two small lagoon ponds associated with the farm are used by 2-3 Canada goose and 2-3 mallard broods each year (W. C. Johnson, *pers. comm.*). These lagoon ponds are approximately 1500 m away from Wintergreen Lake and 2000 m from Gull Lake.

Douglas Lake

Douglas Lake is an alkaline, mesotrophic lake in northern lower Michigan, 45°36'N, 84°42'W, with an approximate surface area of 38 ha and a maximum depth of 9 m (Figure 2). Recreation and fishing use is moderate, and there are about 75 cottages on the lakeshore. In addition, the University of Michigan Biological Station is located on the southernmost shore. Approximately 5 broods of mallards, 1-3 broods of wood ducks, and 1-3 broods of common mergansers are produced on Douglas Lake each year (H. D. Blankespoor, *pers. comm.*).

Field Methods

Waterfowl capture and sampling

Wild waterfowl from the KBS area were captured by drive trap and bait trap and sampled for blood hematozoa in summer 1995 (June 1-August 24). These birds were from all three KBS areas (Gull Lake, Kellogg Bird Sanctuary, and Kellogg Farm). Drive traps consist of a V-shaped fence into which waterfowl are driven. The point of the V opens into a small corral from which the waterfowl are removed by hand. A bait trap consists of a wire cage with openings that allow easy entry but make escape difficult. These were partially submerged near the shores of Wintergreen Lake and baited with corn. Additionally, wild waterfowl from Wintergreen Lake were captured by bait trap and sampled in fall 1995 (September 9-October 8).

Captive waterfowl belonging to the Kellogg Bird Sanctuary were also sampled during summer 1995. Many of these were restricted to outdoor pens; others were free-ranging but clipped wing feathers or previous injuries restricted them from moving outside the Sanctuary. Common mergansers were captured by drive trap from Douglas Lake on July 17, 1995.

Upon capture, the species, age, and sex of each bird were determined. Sampled waterfowl were assigned to one of three age classes. After-hatch-year (AHY) birds are those that hatched in 1994 or before and have thus completed one or more migrations to wintering grounds. Hatch-year (HY) birds are those that hatched in 1995 but had attained flight at the time of sampling. Although HY waterfowl may have hatched in the area of sampling, it is also possible that they hatched elsewhere. Local (L) birds are those that hatched in 1995 in the area they were sampled and had not yet attained flight at the time of sampling.

Blood was drawn via metatarsal vein puncture with a sterile lancet. Two thin blood smears were made from each bird. Birds without bands were fitted with a U.S.

Fish and Wildlife Service (USFWS) band and then released. Birds already possessing bands were recorded and released.

Sentinel ducklings

A total of 186 ducklings was used throughout the summer to assess whether transmission of waterfowl blood parasites occurred in the KBS area. Sentinels used in the study were black ducks, mallards, wood ducks, and domestic mallards. These birds were obtained either from eggs hatched in the laboratory, or as 1-3 day old "orphans" which were brought to the Sanctuary by the public. All sentinels were raised in the laboratory until they were 14-17 days old, where exposure to vectors was severely limited. They were then placed in outdoor pens (breeding pens of the Sanctuary) for the next 7-14 days, where they were accessible to potential vectors and located approximately 50 m from Wintergreen Lake. The next 20-22 days were spent in cages (also accessible to potential vectors) partially submerged in the lake, approximately 3 m from the shore. This exposure regime allowed for at least one group of sentinels to be exposed for nearly every date between May 30 and September 1.

Following exposure, each group of experimental birds was sampled for blood parasites. Blood smears were made as for wild waterfowl. Experimental birds, except domestic mallards, were banded and released after sampling. Eighteen domestic mallards were banded with non-USFWS bands, placed back into the outdoor pens at the Sanctuary on July 20, and resampled on August 31. This provided an additional test of whether transmission of any blood parasites occurred.

Vector collection

Two variations of the Bennett trap (Bennett, 1960), which utilized live ducks as attractants, were used in collecting waterfowl-feeding flies. The first, similar to the original trap (Bennett, 1960), consisted of two portions: the holding cage for bait birds,

and the collecting cage for insects (Figure 3). The holding cage was 30 X 30 X 30 cm and made of 1-inch mesh vinyl-coated wire cloth. The top of the holding cage was hinged, providing access to the inside of the cage. Feed and water dishes were wired to one side. The collecting cage consisted of a 60 X 60 X 60 cm wood frame covered by fine nylon screen (250-micron mesh) on five sides, leaving the bottom open. Strips of sponge rubber were adhered to the bottom of the collecting cage to prevent flies from escaping. Bait birds were provided with food and water and placed in the holding cages, and set on a plywood square near the lakeshore at about one hour before sunset. Forty minutes later, the collecting cage was placed over the bait duck by hand or it was lowered from above using a rope slung over a tree branch. Engorged and unengorged flies were collected in an aspirator through a sleeve in the top of the collecting cage and identified later. This process of exposure and collection was repeated at sunset.

The second Bennett trap variation used was similar to that of Meyer and Bennett (1976). Four polythene funnels of about 25 cm diameter were inserted in two sides of the screened frame (Figure 3). The narrow stems of the funnels were removed, leaving entrance holes of 5 cm in diameter at the base of the funnels. Bait birds provided with food and water were placed in the holding cage (described above) within these traps at 1800-1900 hours and left until the following morning (approximately 0800 hours). Engorged and unengorged flies were collected and preserved as above. Both Bennett trap variations were used on calm, dry nights on the following 23 dates: June 6, 7, 18, 19, 21, 25, 28; July 2, 3, 4, 5, 8, 9, 10 , 21, 23, 24, 27, 29, 31; August 6, 12, 13. Four locations near the shore of Wintergreen Lake were used, alternating location each collection night.

Figure 3. Diagrammatic representation of Bennett trap, consisting of insect trap and bait-bird holding cage. Two variations of insect trap were used. In the first the insect trap was placed over the bird from above after 40 minutes exposure. In the second, funnels were added as entrances for insects and the insect trap placed over the bird for the entire night.

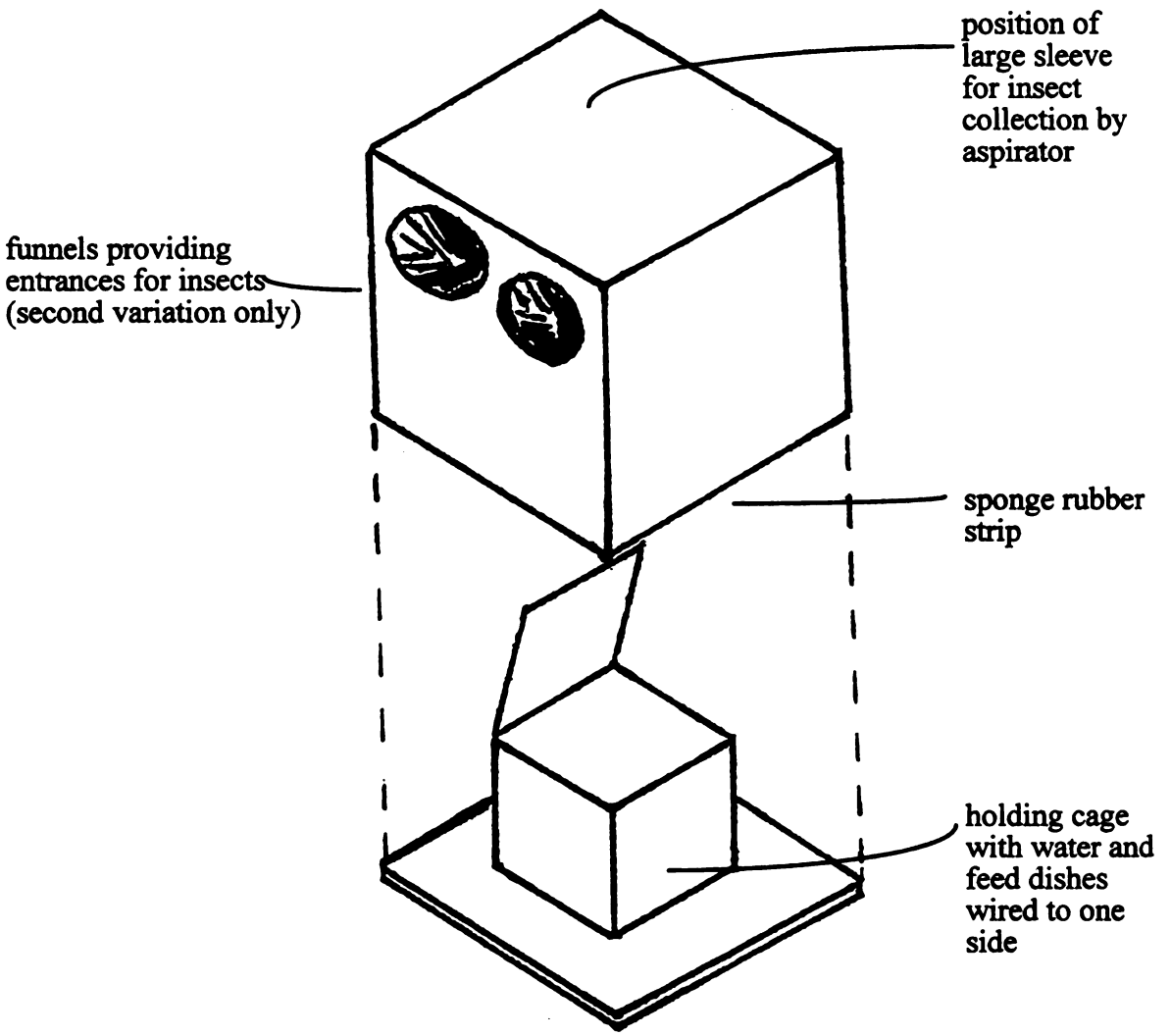
position of large sleeve for insect collection by aspirator
funnels providing entrances for insects (second variation only)
sponge rubber strip
holding cage with water and feed dishes wired to one side

Figure 3.

Laboratory Methods

Blood smears were air-dried, fixed in methanol, and stained with Fisher Scientific LeukoStat™ Stain Kit (Fisher Scientific, Pittsburgh, PA, 15219). The results of LeukoStat do not differ markedly from Giemsa's stain with the exception of the cytoplasm of microgametocytes, which stains red instead of light blue. Therefore, parasites identified in this study were comparable to the descriptions above. To determine prevalence of hematozoans, blood smears were first scanned at 200X magnification so that both smears were examined in their entirety (most gametocytes and schizonts are easily seen at this magnification). Then they were examined at 1000X magnification for 10 minutes each so that a total of 20 minutes was expended to examine both slides from each bird, allowing scanning of about 250-350 fields of view, resulting in an estimated 15,000-25,000 erythrocytes scanned. Prevalence is defined as the number of birds infected with a particular hematozoan species divided by the number of birds examined, in accordance with Margolis et al. (1982). Overall hematozoan prevalence is defined as the number of birds infected with any hematozoan species divided by the number of birds examined.

Quantification of hematozoans generally followed the recommendations of Godfrey et al. (1987) and Fedynich et al. (1995). If hematozoans were present, the best slide was selected (based on smear thickness and staining) and 5,000 erythrocytes were counted in 50 replicates of 100 erythrocytes each (at 400X) to provide an estimate of parasite intensity within each infected bird. Each count of 100 erythrocytes (one replicate) was obtained using one or more different fields of view delineated by the large square of a Miller ocular disc. A random number table was used to determine the number of fields skipped between each field of view examined. If the field of view was inadequate for examination (e.g., too thick) the smear was advanced to the next suitable field of view. Intensity is defined as the number of erythrocytes infected by a parasite

species divided by 5,000 erythrocytes counted in a particular host, in accordance with Margolis et al. (1982). Intensities <1/5,000 erythrocytes were arbitrarily assigned a value of 0.5 so that they could be included in analysis (Godfrey et al., 1990; Fedynich and Rhodes, Jr., 1995).

Leucocytozoon spp. have rarely been quantified on blood smears (Allan and Mahrt, 1989; Fedynich and Rhodes, Jr., 1995) because of concern over potential pooling of this parasite on the smear and because *Leucocytozoon* spp. infect leukocytes in addition to erythrocytes (Godfrey et al., 1987; Fedynich et al., 1995). However, it is possible to test if *Leucocytozoon* gametocytes vary concordantly with erythrocyte densities (Fedynich and Rhodes, Jr., 1995). Based on regression analysis from a subsample of ten smears from ten common mergansers from Douglas Lake, *Leucocytozoon simondi* densities varied concordantly with erythrocyte densities. Thus, pooling does not appear to be a significant factor and the number of *L. simondi* gametocytes per 5000 infected erythrocytes is an accurate measure of intensity.

Data Analyses

Contingency analyses were used to analyze KBS prevalence data and the effects of host species, age, sex, and season. For this analysis, black ducks and black-duck mallard hybrid data were removed because of the small number of birds captured. Douglas Lake prevalences were compared between sexes using contingency analysis. Comparisons between KBS summer data and Douglas Lake data were made using contingency analyses of overall hematozoan prevalence and the prevalences of hematozoan species occurring in both areas.

A regression analysis was performed on waterfowl age in years and overall hematozoan prevalence. For this analysis, minimum waterfowl age in years was

determined. Local birds were arbitrarily given an age of 0.1 years, HY birds, 0.2 years, and AHY birds, 1 year unless possessing a band when captured. Ages of birds already possessing bands at the time of sampling were determined using the banding records of the Kellogg Bird Sanctuary and the USFWS. If the bird originally received its band as an adult, only the minimum age of the bird could be determined.

Because intensity data were not normally distributed, Kruskal-Wallis tests or Mann-Whitney U tests were used in their analysis. Comparisons were made between mean intensities in KBS waterfowl for host species, ages, sexes, and seasons. Douglas Lake mean intensities between waterfowl sexes were compared. Mean intensities of hematozoan species common to both locations were also compared (using KBS summer data only). All statistical analyses were performed using SYSTAT For Windows, v.6.0.1 (SPSS, Inc., 1996).

RESULTS

Waterfowl sampled

In total, five species of wild waterfowl were sampled from the KBS area: three black ducks, 77 Canada geese, 220 mallards, two mallard-black duck hybrids, and 30 wood ducks (Table I). The most important differences between the summer and fall samples are the absence of Canada geese in the fall sample and the natural absence of the L age class in the fall sample. Fifty-five L common mergansers were sampled from Douglas Lake.

Hematozoa of KBS summer waterfowl

Three hemosporid species, *Haemoproteus nettionis, H. greineri,* and *Leucocytozoon simondi* were identified from wild waterfowl (Table II). Overall hematozoan prevalence was 5.5 %. *Haemoproteus nettionis* was the most common parasite species infecting 4.1 % of waterfowl. *Leucocytozoon simondi* and *H. greineri* infected 1.8 % and 0.5 % respectively. One mallard was infected with both *H. nettionis* and *L. simondi*, and one wood duck was infected with both *H. nettionis* and *H. greineri.* Canada geese were infected with only one hematozoan, *H. nettionis.*

Low prevalences of individual hemosporid species precluded statistical analysis of the effects of host-intrinsic factors on prevalence data within each host species. However, using overall hematozoan prevalence, comparisons between waterfowl species could be made and no differences were found (after removing black duck data because of

Table I. Number of waterfowl by species, age, and season sampled from KBS.

	Summer*				Fall†				
Species	L‡	HY	AHY	Subtotal	L	HY	AHY	Subtotal	Total
Black duck	0	0	1	1	0	1	1	2	3
Canada goose	49	0	28	77	0	0	0	0	77
Mallard	73	14	32	119	0	77	24	101	220
Mallard-black duck hybrid	0	0	0	0	0	0	2	2	2
Wood duck	1	10	10	21	0	3	6	9	30
Total	123	24	71	218	0	81	33	114	332

*June 1-August 24, 1995
†September 9-October 8, 1995
‡L=Local, HY=Hatch-year, AHY=After-hatch-year

Table II. Prevalence of hematozoa in KBS summer waterfowl.

Bird species	N*	All hematozoa	*Haemoproteus nettionis*	*Haemoproteus greineri*	*Leucocytozoon simondi*
Black duck	1	0.0 % (0)†	0.0 % (0)	0.0 % (0)	0.0 % (0)
Canada goose	77	3.9 % (3)	3.9 % (3)	0.0 % (0)	0.0 % (0)
Mallard	119	6.7 % (8)	4.2 % (5)	0.0 % (0)	3.4 % (4)
Wood duck	21	4.8 % (1)	4.8 % (1)	4.8 % (1)	0.0 % (0)
Total	218	5.5 % (12)	4.1 % (9)	0.5 % (1)	1.8 % (4)

*Number of birds examined
†Prevalence (Number of birds infected)

Table III. Overall hematozoan prevalence by age class in KBS summer waterfowl.

Waterfowl age class	N*	All hematozoa
L†	123	0 % (0)‡
HY	24	8.3 % (2)
AHY	71	14.1 % (10)
All classes	218	5.5 % (12)

*Number of birds examined
†L=Local, HY=Hatch-year, AHY=After-hatch-year
‡Prevalence (Number of birds infected)

small sample size, chi-square analysis, $X^2 = 0.8$, $P > 0.05$). Therefore, data from different waterfowl species could be combined and comparisons between waterfowl age and sex classes could be made statistically. No L waterfowl were infected with any blood parasite (Table III). Overall hematozoan prevalence did not differ significantly between HY and AHY age classes ($X^2 = 2.1$, $P > 0.05$) or between sexes ($X^2 = 0.4$, $P > 0.05$).

Mean intensities of hemosporids are in Table IV. The low prevalences of hematozoans precluded statistical analysis of the effects of host-intrinsic factors on intensity data within each host species. Mean intensities of *H. nettionis* (the only parasite species to infect multiple host species) did not differ between waterfowl species (Kruskall-Wallis test, $W = 1.9$, $P > 0.05$). When waterfowl species were combined, host-intrinsic factors were analyzed using intensity data, but no significant differences were found for mean intensities of any parasite between waterfowl ages or sexes (Mann-Whitney U-tests, $U = 1.0, 6.0$, $P > 0.05$).

Thirty-five captive waterfowl of native and exotic species were sampled for blood parasites during the summer (Table V). None were found to be infected with any blood parasites.

Hematozoa of KBS fall waterfowl

The same three hemosporid species were found in waterfowl sampled in the fall as in summer waterfowl (Table VI). Four dual infections occurred in mallards; two were infected with *H. nettionis* and *H. greineri* and two were infected with *H. nettionis* and *L. simondi*. In addition, one mallard was infected with three parasites, *H. nettionis*, *L. simondi*, and an unidentified microfilaria. Fall waterfowl had an overall hematozoan prevalence of 11.4 %, about 2X that of summer waterfowl (5.5 %), but this difference was only marginally significant ($X^2 = 2.9$, $P = 0.09$). Prevalences of the three hemosporid

Table IV. Mean intensity of hemosporids from KBS summer waterfowl.

Waterfowl species	*Haemoproteus nettionis*	*Haemoproteus greineri*	*Leucocytozoon simondi*
Canada goose	4.7±2.2* (2-9)† 3‡	—§	—
Mallard	5.2±1.6 (1-10) 5	—	0.9±0.1 (0.5-1) 4
Wood duck	1.0 (1) 1	0.5 (0.5) 1	—
Total	4.6±1.1 (1-10) 9	0.5 (0.5) 1	0.9±0.1 (0.5-1) 4

*Mean intensity ± standard error of hemosporids/5,000 erythrocytes
†(Range)
‡Number of birds infected
§None infected

Table V. Species and number of captive waterfowl sampled from the Kellogg Bird Sanctuary.

Species	Number sampled
Black duck-northern pintail hybrid	2
Black swan	5
Domestic mallard	6
Domestic greylag goose	1
Mallard	1
Mute Swan	4
Trumpeter Swan	16
Total	35

Table VI. Prevalence of hematozoa in KBS fall waterfowl.

Bird species	N*	All hematozoa	*Haemoproteus nettionis*	*Haemoproteus greineri*	*Leucocytozoon simondi*	Microfilaria
Black duck	2	50.0 % (1)†	0.0 % (0)	0.0 % (0)	50.0 % (1)	0.0 % (0)
Mallard	101	9.9 % (10)	7.9 % (8)	1.9 % (2)	5.0 % (5)	1.0 % (1)
Mallard-black duck hybrid	2	50.0 % (1)	0.0 % (0)	50.0 % (1)	0.0 % (0)	0.0 % (0)
Wood duck	9	11.1 % (1)	0.0 % (0)	11.1 % (1)	0.0 % (0)	0.0 % (0)
Total	114	11.4 % (13)	7.0 % (8)	3.5 % (4)	5.3 % (6)	0.9 % (1)

*Number of birds examined
†Prevalence (Number of birds infected)

species were comparable; *Leucocytozoon simondi, H. nettionis*, and *H. greineri* infected 5.3 %, 4.4 %, and 3.5 % of waterfowl, respectively.

Low prevalences of individual hemosporid species precluded statistical analysis of the effects of host-intrinsic factors on prevalence data within each host species. Using prevalences of all hematozoa combined, comparisons between species could be made statistically and no significant differences were found ($X^2 = 6.12$, $P > 0.05$). By combining host species data, statistical comparisons between waterfowl age and sex classes could be made. Significant differences were not found for overall prevalence between age or sex classes ($X^2 = 0.3, 0.6$, $P > 0.05$).

Regression analysis showed a significant linear relationship between waterfowl <3 years of age (ages ≥ 3 were removed because of small sample sizes) and overall hematozoan prevalence ($r^2 = 0.75$, $P = 0.00000$). A similar significant relationship existed when ages ≥ 3 were added to the analysis ($r^2 = 0.37$, $P = 0.00000$; Figure 4). The boxed insert in Figure 4 lists the number of birds sampled for each age.

Low prevalences precluded statistical analysis of the effects of host-intrinsic factors on fall intensity data within each host species (Table VII). Low prevalences also precluded statistical analysis to test for differences in mean intensity between host species. When all waterfowl species were combined, no significant differences were found for parasite mean intensities between waterfowl ages or sexes ($U = 0.5, 7.0$, $P > 0.05$). Mean intensity of *H. nettionis* was significantly higher in the summer than in the fall ($U = 47.0$, $P = 0.01678$). No differences in mean intensities existed between seasons for *H. greineri* or *L. simondi* ($U = 0.0, 15.0$, $P > 0.05$).

Figure 4. Relationship between age and overall hematozoan prevalence in KBS waterfowl. Boxed insert in upper left lists the number of waterfowl sampled in each age group. In the lower right is the regression equation and coefficient.

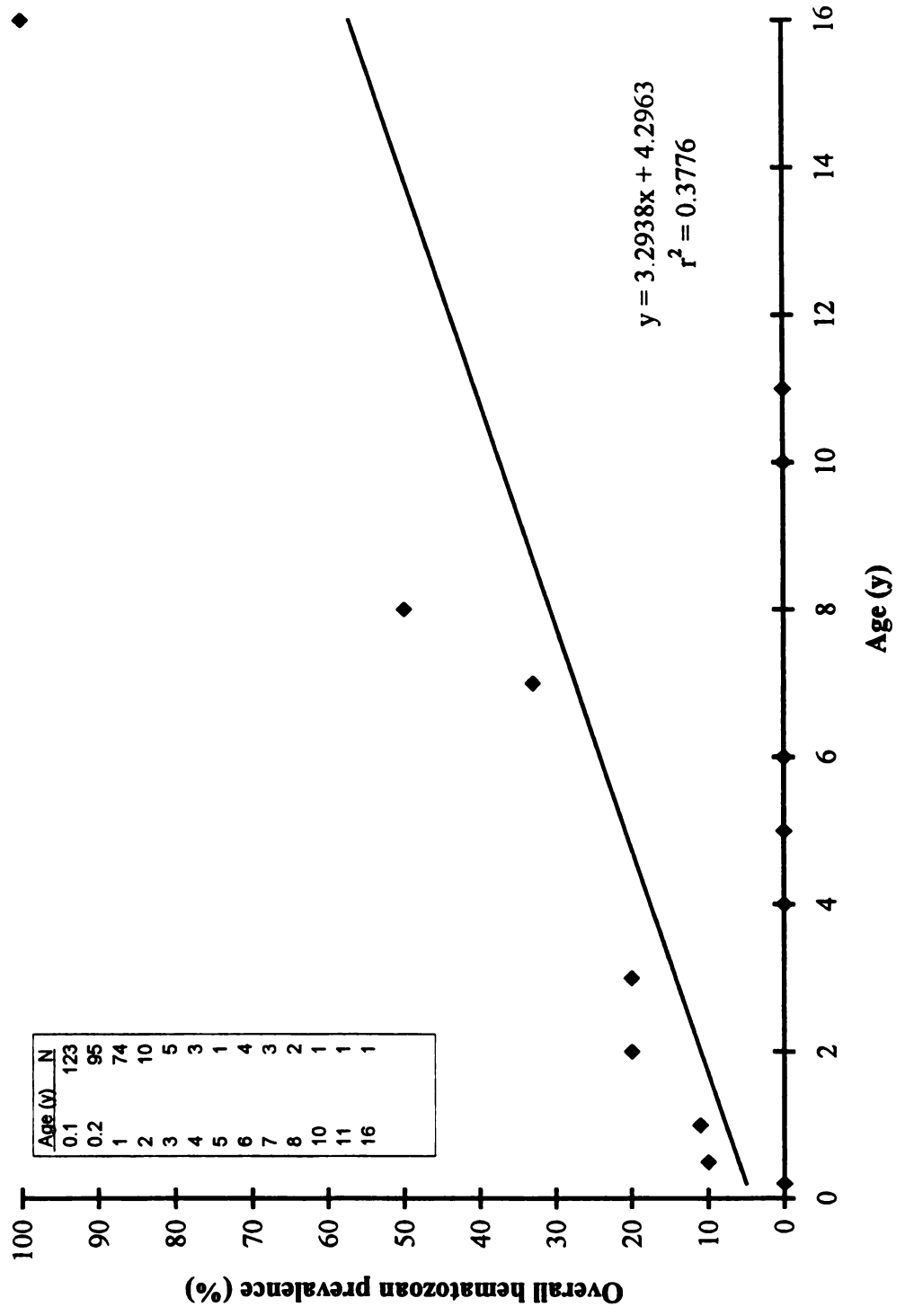
Overall hematozoan prevalence (%)
Age (y)
y = 3.2938x + 4.2963
r² = 0.3776
Age (y) N
0.1 123
0.2 95
1 74
2 10
3 5
4 3
5 1
6 4
7 3
8 2
10 1
11 1
16 1

Figure 4.

Table VII. Mean intensity of hemosporids in KBS fall waterfowl.

Waterfowl species	*Haemoproteus nettionis*	*Haemoproteus greineri*	*Leucocytozoon simondi*
Black duck	—*	—	0.5 (0.5) 1
Mallard	1.3±0.2† (0.5-2)‡ 8§	4.0±0.0 (4) 2	0.8±0.1 (0.5-1) 5
Mallard-black duck hybrid	—	1.0 (1) 1	—
Wood duck	—	1.0 (1) 1	—
Total	1.3±0.2 (0.5-2) 8	2.0±0.7 (1-4) 4	0.8±0.1 (0.5-1) 6

*None infected
†Mean ± standard error of hemosporids/5,000 erythrocytes
‡(Range)
§Number infected

Hematozoa of Douglas Lake common mergansers

Three species of hemosporids were identified, *H. greineri, L. simondi*, and *Plasmodium circumflexum* with prevalences of 50.9 %, 47.3 %, and 3.6 %, respectively (Table VIII). Overall hematozoan prevalence was 74.6 %. Thirteen common mergansers (23.6 %) were infected with *H. greineri* and *L. simondi*. Two (3.6 %) dual infections with *H. greineri* and *P. circumflexum* occurred. Prevalences did not differ between sexes for overall hematozoan prevalence or for prevalences of each parasite species individually (X^2 = 0.005-2.2, $P > 0.05$). *Plasmodium circumflexum* prevalences were not analyzed because only two birds were infected.

Mean intensities of *H. greineri* and *L. simondi* were not significantly different (U = 443.5, $P > 0.05$; Table IX). However, *H. greineri* mean intensity in single infections (*H. greineri* only) was significantly greater than *H. greineri* mean intensity in dual infections with *L. simondi* (U = 123.5, $P = 0.03954$). *Leucocytozoon simondi* mean intensities did not differ between single and dual infections with *H. greineri* (U = 80.0, $P > 0.05$). One bird infected with *L. simondi* had an intensity of 78/5,000 erythrocytes, much higher than any other bird. The difference in *H. greineri* intensity between single and dual infections with *L. simondi* remained the same whether this outlying data point was removed or retained in the analysis. The statistical tests reported above and Table IX include the outlier.

Mean intensities of either *H. greineri* or *L. simondi* did not differ significantly between host sexes (U = 74.5-95.0, $P > 0.05$). *Plasmodium circumflexum* mean intensity was 1.25/5,000 erythrocytes, with a range of 0.5-2, and was excluded from statistical analysis because of the low number of birds infected.

Compared to overall hematozoan prevalence at KBS, Douglas Lake overall prevalence was significantly higher (X^2 = 149.8, $P = 0.00000$). When analyzed

Table VIII. Prevalence of hematozoans in 55 L Douglas Lake common mergansers.

All hematozoa	*Haemoproteus greineri*	*Leucocytozoon simondi*	*Plasmodium circumflexum*
74.6 % (41)*	50.9 % (28)	47.3 % (26)	3.6 % (2)

*Prevalence (Number of birds infected)

Table IX. Mean intensity of single and dual infections in Douglas Lake common mergansers.

Infection type	*Haemoproteus greineri*	*Leucocytozoon simondi*
Single	4.0±1.1*	7.4±5.9
	(0.5-13)†	(0.5-78)
	13‡	13
Dual	1.5±0.4	1.6±0.5
	(0.5-5)	(0.5-6)
	13	13
Total	2.9±0.6	4.5±3.0
	(0.5-13)	(0.5-78)
	26	26

*Mean ± standard error of hemosporids/5,000 erythrocytes
†(Range)
‡Number of birds infected

individually, parasite species common to both locations (*H. greineri* and *L. simondi*) had significantly higher prevalences at Douglas Lake ($X^2 = 147.6$, *H. greineri*; $X^2 = 109.6$, *L. simondi*; $P = 0.00000$). Mean intensities of these two common species did not differ between locations ($U = 4.5, 53.5, P > 0.05$).

Sentinel ducklings

None of the 186 ducklings used as sentinels at KBS became infected with any blood parasite. Of eighteen sentinels resampled on August 31, none were infected with any blood parasite.

Vector collections

Bennett traps caught only two species of mosquito, *Coquillittidia perturbans* and *Culex tarsalis*, capturing 310 and 89 individuals respectively. Engorged and unengorged individuals of both species were captured. Neither biting midges or black flies were captured nor ever seen feeding on KBS waterfowl.

DISCUSSION

Kellogg Biological Station

The three hemosporid species found in KBS waterfowl have been previously reported from northern Michigan waterfowl (O'Roke, 1931, 1934; Herman et al., 1975, Desser et al., 1978; Sibley and Werner 1984) but not from southern Michigan waterfowl. Thus, the present study is the first survey of waterfowl at KBS and in southern Michigan. Sibley and Werner (1984) did not survey wild waterfowl but did report natural transmission of *H. nettionis* to domestic ducks in the upper peninsula of Michigan. They also noted gametocytes which completely encircled the host cell nucleus in addition to halteridial gametocytes, but identified all of them as *H. nettionis*, since *H. greineri* had not yet been described (described in Bennett et al., 1984). Therefore, it can be suggested that *H. greineri* also was transmitted in their study. Bennett et al. (1984) stated that *H. greineri* was endemic to the prairie regions of Canada, but my analysis of Sibley and Werner's (1984) results show that the transmission range of this parasite also includes the upper peninsula of Michigan. In addition, a recent study extended the known transmission range of *H. greineri* to include eastern Canada and northeastern United States (Pung et al., 1997). In the present study, none of the birds infected with *H. greineri* were local, so it is not clear if southern Michigan is part of the transmission range of this parasite.

Compared to other surveys of Michigan waterfowl, prevalences of hematozoans in the KBS area were low. Herman et al. (1975) reported *L. simondi* as the causative agent of Canada geese gosling mortality at the Seney National Wildlife Refuge in the upper peninsula. They reported prevalence as 80 % in AHY geese just prior to egg-

laying and 100 % in goslings each year. They also reported the presence of *H. nettionis*, *Plasmodium* spp., and trypanosomes, but stated that prevalences were low compared to *L. simondi*. O'Roke (1931, 1934) found that 100 % of black ducks and mallards were infected in the Douglas Lake vicinity and 30 % of black ducks were infected in the Munuscong Lake vicinity, which lies between Lake Huron and Lake Superior.

Compared to other North American studies of waterfowl hematozoa, the overall prevalences of hematozoans in the KBS area in the summer (5.5 %) and fall (11.4 %) were low. Although a wide range of overall hematozoan prevalences has been reported for different localities in North America (0-100 %), similarly low prevalences have been reported from only a few localities during the summer and early fall. Burgess (1957) reported only one hematozoan species, *L. simondi*, infecting <1 % of waterfowl from several areas in Saskatchewan and Manitoba. An overall hematozoan prevalence of 3 % was reported in snow and Canada geese from the Northwest Territories (Bennett and MacInnes, 1972). Blood parasites were not found in waterfowl from eastern Newfoundland (Bennett and Inder, 1972; Bennett et al., 1991). Bennett et al. (1982) reported an overall prevalence of 9 % from one region in Saskatchewan. Thul et al. (1980) reported an overall prevalence of <1 % in wood ducks from southeastern states and O'Dell and Robbins (1994) reported an overall prevalence of 10 % in wood ducks in Missouri. Most authors attribute low prevalences during the summer and early fall months to an absence or low abundance of vectors. In eastern Newfoundland, the absence of vectors is attributed to the steady easterly winds that blow off the Atlantic Ocean (Bennett and Inder, 1972; Bennett et al., 1991). Other authors do not explain the absence or low abundance of vectors.

Other North American studies have reported higher prevalences (>25 %) in waterfowl during the summer and early fall in the following regions: northeastern U.S. (Nelson and Gashwiler, 1941; O'Meara, 1956; Herman et al., 1971; Bennett et al., 1974; Thul et al., 1980), maritime Canadian provinces (Bennett et al., 1975; Bennett et al.,

1991), Alberta and Saskatchewan (Williams et al., 1977; Bennett et al., 1982), Northwest Territories (Williams et al., 1977).

A few other studies have reported an absence (Michot et al., 1995) or low prevalence (≤16 %; Levine and Hanson, 1953; Bradshaw and Trainer, 1966; Kocan et al., 1979; Fedynich et al., 1993) in migrating waterfowl during the late fall and in wintering waterfowl. However, low prevalences in late fall and winter are expected because infections can go undetected due to low intensities (Fedynich et al., 1993) whereas infections are expected to be more readily detected during the summer and early fall because intensities are higher.

In the avian blood parasite literature, many authors compare survey results to the summary regional data in Greiner et al. (1975a), who arbitrarily divided North America into seven topographical regions which varied in overall prevalence of avian hematozoa as well as in the relative frequencies of the three hemosporid genera. The Great Lakes area was included in a region which had a moderately high overall prevalence (38 %; ranked third amongst the seven regions) and prevalences of *Leucocytozoon* spp., *Haemoproteus* spp., and *Plasmodium* spp. were 23 %, 18 %, and 4 %, respectively. Prevalences at KBS were low comparatively, but the summary regional data of Greiner et al. (1975a) is for all bird families combined, and therefore is of only limited benefit in comparison to data from the Anatidae only.

Greiner et al. (1975a) also summarized prevalence data by family and species, and reported that the overall hematozoan prevalence for north american Anatidae was 31.9 % with prevalences of *L. simondi*, *Haemoproteus* spp., and *Plasmodium* spp. 15.5 %, 19.5 %, and 2.9 %, respectively. The overall prevalence for mallards was 27 % with prevalences of *L. simondi*, *Haemoproteus* spp., and *Plasmodium* spp. 11.3 %, 15.6 %, and 1.7 %, respectively. For wood ducks, the overall prevalence was 55.4 %, with prevalences of *L. simondi*, *Haemoproteus* spp., and *Plasmodium* spp. 21.8 %, 49.9 %, and 5.3 %, respectively. For Canada geese, the overall prevalence was 6.5 %, with

prevalences of *L. simondi*, *Haemoproteus* spp., and *Plasmodium* spp. 4.0 %, 2.1 %, and 0.2 %, respectively. Except for Canada geese, KBS prevalences are low compared to these summary data. However, the Canada geese data in Greiner et al. (1975a) may be biased by location and do not include any data from the Michigan upper peninsula, where Canada geese have very high prevalences of hematozoa (Herman et al., 1975).

Species richness values of the KBS hemosporid community in both summer (3) and fall (3) were moderate compared to other studies of North American waterfowl. The number of hemosporid species reported ranges from zero to six and averages 2.6 (my own analysis of 22 of the above studies).

Intensities of hemosporids in KBS summer waterfowl were low (Table IV), an expected result because low intensities are indicative of chronic infections (Allan and Mahrt, 1989) and 10 of the 12 birds infected were adults. It is possible that these infected birds had earlier suffered spring relapses, but sampling occurred late enough in the summer that intensities were probably returning to chronic levels. The difference between seasons in the mean intensity of the most common parasite, *H. nettionis* (Tables IV and VII) is expected since fall intensities should be close to the chronic infection state and summer intensities should be somewhere between the extremely high intensities caused by spring relapse and the low intensities of chronic infection. The lack of a seasonal difference for *H. greineri* or *L. simondi* mean intensities may be due either to the small number of birds infected or that birds infected with these parasites were captured toward the end of the summer period.

Most authors only give rough estimates of hemosporid intensity in wild waterfowl, without quantifying intensity per number of counted erythrocytes. For example, many investigators estimate intensity by counting the number of parasites per minutes expended examining the smear. These kinds of estimates are not regarded as accurate by some researchers (Godfrey et al., 1987; Fedynich et al., 1995), but broad comparisons can be made to the present study. O'Roke (1934) and Herman et al. (1975)

noted high intensities of *L. simondi*, much higher than mean intensities in KBS waterfowl, during the breeding season. Estimates given for summer waterfowl sampled after breeding are similar to the *H. nettionis* mean intensity for KBS summer waterfowl (Herman et al., 1971; Williams et al., 1977; O'Dell and Robbins, 1994). Estimates given for wintering waterfowl (Trainer et al., 1962; Polcyn and Johnson, 1968; Kocan and Knisley, 1970) are lower than *H. nettionis* mean intensity for KBS summer waterfowl and are similar to or slightly lower than that for KBS fall waterfowl. Only Fedynich et al. (1993) quantified intensity of waterfowl hemosporids using methods similar to mine, and they report a *H. nettionis* mean intensity of waterfowl wintering in Texas (1.6±0.1, mean ± standard error of gametocytes/5,000 erythrocytes) which is similar to *H. nettionis* mean intensities in KBS fall waterfowl (1.2±0.3), but lower than in KBS summer waterfowl.

The component community of hematozoa in KBS waterfowl can be characterized as depauperate, having moderate species richness but low prevalences and intensities. Therefore, the metapopulations of each parasite species appear to be small. This is a somewhat surprising finding given the large, high-density waterfowl populations and the abundance and variety of aquatic habitats suitable for vector larvae in the KBS area. The low prevalences and intensities and the low number of multiple infections suggest that species interactions are few or non-existent. Thus the component community of hemosporids in KBS waterfowl can also be characterized as isolationist. Similarly, Fedynich et al. (1993) classified the hemosporid community of waterfowl wintering in south Texas as isolationist based on low prevalences, low intensities, and low number of multiple infections.

Parasite transmission is critical to the structure of metapopulations and component communities. One expects low transmission rates in an isolationist community, because they lead to unsaturated, nonequilibrium communities that provide few opportunities for interspecific interactions (Holmes and Price, 1986). There is strong evidence from my study to indicate that transmission does not occur in the KBS area. First, hematozoans

were absent from 123 wild L waterfowl sampled. Secondly, 35 captive waterfowl, which are year round residents of the Kellogg Bird Sanctuary, were hematozoan free. Finally, none of the 186 sentinel ducks exposed over the course of the summer became infected with any hematozoan. The five week exposure period should have allowed ample time for the development of hemosporids since the longest time required for patency in ducks is 14-19 days for *Plasmodium* spp. (Meyer et al., 1974).

Transmission appears not to occur because of a lack of vectors. While *Culex tarsalis* is known to be a vector of *P. relictum* (see Work et al., 1990), no *Plasmodium* spp. were found in KBS waterfowl. *Coquillittidia perturbans* is not known to vector any avian blood parasite.

It is not surprising that black flies were never seen or captured feeding on waterfowl because their larval habitat requirements are restricted to swift, oxygenated streams which are uncommon in the KBS area. In fact, Kocan and Clark (1966a, 1966b) housed their experimental waterfowl at KBS because *L. simondi* was assumed not to be transmitted there. I did find black fly larvae near the outlet of Wintergreen Lake, but these were present only at the beginning of the summer. The site at which I found them was an unnatural one, where water was rushing over a recently installed water level control gate, which had not existed in previous years (W. C. Johnson, *pers. comm.*). Although I did not attempt to identify these larvae, they were likely *Simulium decorum*, a species that commonly colonizes lake outlets (Crosskey, 1990; E. D. Walker, *pers. comm.*).

It is surprising that no ceratopogonids were ever seen or captured feeding on waterfowl, since their larval habitats are very diverse. While waterfowl-feeding species were not present, it is possible that other ceratopogonids were present at KBS. No other surveys have been done of hematophagous insects in the KBS area (E. D. Walker, *pers. comm.*).

The only host-intrinsic factor for which any significant differences were found in KBS waterfowl was age. This was due to the lack of transmission in the KBS area. Infected AHY waterfowl breeding in the KBS area probably did not obtain hemosporid infections in the KBS area, but instead may have obtained them during migration or on wintering areas. It is known that some of the KBS waterfowl winter as far south as Missouri and Tennessee (Kellogg Bird Sanctuary banding records) where transmission may occur in the early fall or begin in the spring before the birds leave on their northward migrations. The high vagility of waterfowl probably plays a role in the structure of their hematozoan communities.

The significant relationship between overall prevalence and waterfowl age in years was not unexpected (Figure 4). It is known that birds can retain hematozoan infections over many years and it is believed that eradication of the parasite by host immune response is uncommon (Allan and Mahrt, 1989). The gradual increase in prevalence is probably the result of highly vagile birds visiting areas of transmission from time to time.

Although it was not statistically significant, season had an effect on the overall prevalence of hematozoa, with fall overall prevalence being 2X that in summer (Tables II and VI). Many of the waterfowl sampled in the fall were migrants from outside the KBS area, because they did not possess bands when captured. However, because none of the captured birds possessed bands, it was not possible to tell from how far away their breeding sites were. It is believed, however, that most of them were from other areas in southern Michigan (W. C. Johnson, *pers. comm.*). The increase in prevalence in fall waterfowl then, may indicate that hematozoan transmission occurs in other areas in southern Michigan.

Douglas Lake

Two of the hemosporid species identified from Douglas Lake common mergansers, *H. greineri* and *L. simondi,* were also found in KBS summer waterfowl, but prevalences were much higher at Douglas Lake. Overall hematozoan prevalence was also much higher. The high prevalence of *L. simondi* is consistent with the high prevalences previously found at Douglas Lake (O'Roke 1931, 1934) and in other areas of the northern lower and upper peninsulas of Michigan (O'Roke, 1934; Herman et al., 1975). Prevalences in these parts of Michigan are higher than in most parts of North America, but are consistent with the range of prevalences (58-79 %) reported from the northeastern United States and eastern Canada (Nelson and Gashwiler, 1941; O'Meara, 1956; Bennett et al., 1971; Bennett et al., 1974; Thul et al., 1980; Bennett et al., 1991).

Haemoproteus greineri has not been reported in waterfowl from Douglas Lake before and common merganser is a new host record for *H. greineri.* The presence of *H. greineri* in L birds is consistent with my analysis of Sibley and Werner's (1984) results and shows that the transmission range of this parasite is not limited to the prairie provinces of Canada. *Plasmodium circumflexum* occurred at a low prevalence at Douglas Lake, but did not occur in KBS waterfowl. Common merganser is a new host record for *P. circumflexum* and this is the first record of any *Plasmodium* spp. in common merganser. Greiner et al. (1975a) include summary data on the hematozoa of common mergansers and report overall hematozoan prevalence as 41.2 % (14 of 34 infected), with prevalences of *L. simondi* and *Haemoproteus* spp. 8.8 % and 35.3 %, respectively.

Since only L (approximately six weeks old) common mergansers were captured, the high prevalences of *H. greineri* and *L. simondi* indicate that transmission of these species is high, a striked contrast to the KBS area. High transmission rates should lead to more saturated, equilibrium communities with more opportunities for interspecific interactions (Holmes and Price, 1986).

Although species richness of hemosporids was moderate and not higher than for KBS waterfowl, there is evidence that the hemosporid community of Douglas Lake common mergansers is more interactive. Mean intensity of *H. greineri* in single infections was significantly greater than *H. greineri* mean intensity in dual infections with *L. simondi* (Table IX), suggesting that there is some interaction between *H. greineri* and *L. simondi*. The converse relationship did not exist for *L. simondi* mean intensities. It is possible that *L. simondi* has a competitive effect on *H. greineri*. This effect could be due to direct competition, such as competition for host cells, at either the blood stage or the tissue stage of the parasites. On the other hand, the effect may not be the result of direct competition, but instead may be immuno-mediated. Perhaps *L. simondi* evokes a host immune response that is detrimental to *H. greineri*. Another important factor may be which parasite infects the host first, which may depend upon vector emergence periods. Other investigators have noted the potential for interaction between hemosporid species (e.g., Fedynich et al., 1993), but none have reported evidence of interactions. Because of the small sample size in the present study, further investigation is needed to confirm a competitive effect.

High rates of transmission of *L. simondi* to both captive (O'Roke, 1931, 1934; Chernin, 1956a; Barrow et al., 1968) and wild waterfowl (O'Roke, 1931, 1934) have been previously documented at Douglas Lake. O'Roke (1931, 1934) found 100 % of black ducks and mallards (including L and AHY) from Douglas Lake to be infected with *L. simondi*. O'Roke (1931, 1934) believed that wild black duck broods on Douglas Lake were significantly reduced in brood size by mortality caused by *L. simondi*. More recently, based on sampling one brood of L mallards every other year since 1980, H. D. Blankespoor (*pers. comm.*) believes the prevalence of *L. simondi* in mallards on Douglas Lake is close to 100 % and has noticed that brood sizes appear to be reduced by *L. simondi*. Before the present study, it was not known whether L common mergansers from Douglas Lake were infected with *L. simondi*, but it had been noted that L common

mergansers do not suffer the high rate of mortality seen in mallards (H. D. Blankespoor, *pers. comm.*). It is not known why *L. simondi* might be less pathogenic in common mergansers. Diet may be a factor. Common mergansers eat fish almost exclusively, a higher protein and iron source than the invertebrate and vegetation diet of mallards (Bellrose, 1980). Iron may be an especially important mineral in combating anemia, which can be a cause of death in mallards infected with *L. simondi* (Kocan and Clark, 1966b). Another possibility is that common mergansers are less frequently attacked by black flies than are mallards, and therefore do not acquire as many infective sporozoites.

High transmission of *L. simondi* and *H. greineri* indicates abundance of *Simulium* black flies and *Culicoides* biting midges, respectively. *Simulium rugglesi* is the vector of *L. simondi* at Douglas Lake (O'Roke, 1931, 1934; Barrow et al., 1968). Barrow et al. (1968) also reported *Culicoides* spp. feeding on waterfowl at Douglas Lake, but did not identify which species were present. Although it was low, transmission of *P. circumflexum* indicates the presence of *Culex* spp. or *Culiseta* spp. vectors.

CONCLUSIONS

Three hemosporid species were found in KBS waterfowl: *Haemoproteus nettionis* was the most common; *H. greineri* and *Leucocytozoon simondi* were less common. Despite large, high density populations of waterfowl, the hemosporid community of KBS waterfowl has moderate species richness, has low prevalences and intensities, and can be characterized as isolationist. Lack of transmission in the KBS area, due to the absence or low abundance of vectors, is responsible for this isolationist character. Overall hematozoan prevalence at KBS was only 5.5 % in summer waterfowl and 11.4 % in fall waterfowl. The higher prevalence in fall birds may indicate that transmission occurs in other areas of southern Michigan, since many birds sampled in the fall were migratory and had been breeding in other areas.

In contrast, transmission appears to be high at Douglas Lake in northern lower Michigan, resulting in a much higher overall hematozoan prevalence (74.6 %) and more multiple infections. Interactions between hemosporid species would be more likely in a community with such patterns. Mean intensities in Douglas Lake common mergansers were low and similar to those in KBS waterfowl. A possible interaction between *H. greineri* and *L. simondi* is suggested by a significantly lower mean intensity of *H. greineri* in single infections than in double infections with *L. simondi.*

Haemoproteus greineri and *L. simondi* were common, and *Plasmodium circumflexum* was uncommon in Douglas Lake common mergansers. The transmission of *H. greineri* to L common mergansers at Douglas Lake indicates that the range of *H. greineri*, previously thought to be restricted to the prairie provinces of Canada, includes northern Michigan. Common merganser is a new host record for *H. greineri* and *P. circumflexum.*

Breeding waterfowl in northern lower Michigan are similar to those in the northeastern United States and eastern Canada in having high hematozoan prevalences. Hematozoan prevalences in southern Michigan waterfowl are lower than in many areas of North America.

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