INSECT VECTORS AND AVIAN BLOOD PARASITES WITH PARTICULAR REFERENCE TO INSULAR NEWFOUNDLAND

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by

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ABSTRACT

An extensive survey of 14,360 North American birds showing their parasite prevalence and a study of Newfoundland ornithophilic Diptera to determine the incidence of hematozoa in the local avifauna is presented.

The overall infection rate of 55.6% within the North American birds is shown to be concentrated primarily in the passeriform birds and particularly in four families, i.e. Icteridae, Fringillidae, Parulidae and Turdidae. Similarly, the specific blood protozoa which are accountable for the bulk of the infected birds are *Leucocytozoon* and *Haemoproteus*. The incidence of *Plasmodium*, as determined from numbers of infected birds, is of secondary importance in this study.

A stratification performed on the various bird families and species, based on their nesting sites, indicates that the bulk of the infection occurs in the mid canopy levels of the forest environment. A similar situation is observed in the marsh habitats in that there is a higher infection rate among birds whose nests are generally elevated above the marsh surface.

Collections of ornithophilic Diptera (Simuliidae and Ceratopogonidae) from three test sites in Newfoundland verifies that the preferred habitats for these vectors is the 10-15 ft. strata in the woodland environment. Testing over a three year period (1970, 1971 and 1972) indicated a much reduced biting fly population in the

Newfoundland area in comparison to Algonquin Park, Ontario where similar studies had been conducted. The numbers of vector species involved are also noted to be limited. The Hippoboscidae are not considered to be vectors of *Haemoproteus* in Newfoundland.

Examination of the infected glands and hindguts of the ornithophilic Diptera indicated a relatively high incidence of *Leucocytozoon* transmission, a much lower incidence of *Haemoproteus* infection and an almost insignificant *Plasmodium* transmission. With the exception of hippoboscids all vectors were observed to harbour trypanosomes.

A survey of the Newfoundland avifauna verified the parasite prevalence as determined from the laboratory examination of the glands and hindgut of the ornithophilic Diptera. The stratification of the birds supported the premise that most birds became infected in the mid canopy levels, despite some special characteristics of the Newfoundland situation.

It is suggested that in Newfoundland there is a highly developed host-parasite-vector relationship of exceptional efficiency.

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INTRODUCTION

In recent years, a noticeable trend in the study of avian hematozoa has been directed towards elucidation of the life cycle of the parasites in the vertebrate hosts, and relatively little stress has been placed on the epidemiology of the parasitic organisms. The development of this trend is easy to understand, as the epidemiological study is considerably more complex, depending on many factors, including host selection, host range, periodicity, vector range and habitat preference; a most important prerequisite being a full understanding of the host-parasite-vector relationship.

The present study represents an attempt at elucidating some of these factors as they apply to the "relationship". Particular attention is given to habitat preferences of the vector and host and its influence on the prevalence of the specific parasites in the various bird groups.

The research for this thesis was conducted on two different levels and at two different times, viz. on local Newfoundland birds, flies and parasites and on a broader scale - the avian hematozoa of North America. Consequently, the thesis is presented in two parts.

Part I - The relationship of the breeding biology of North American Birds and the feeding behavior of the vectors of avian hematozoa.

Part II - The feeding behavior of the vectors of avian hematozoa of insular Newfoundland. Thus, the underlying principle throughout is a study of the host-parasite-vector relations, brought about by a relatively broad study whose principles can be realized on a much more restricted local level.

HISTORICAL

The interest or concern in the avian blood parasites commenced around the time of Danilewsky (born 1852) in Kharkov, U.S.S.R. As a profession, he chose medicine, having received a medical degree from the University of Kharkov in 1877. His credentials as a scientist recognizes him as a great physiologist rather than the first avian malariologist. However, his brief contact with this field has left a lasting impression.

It is fortunate for present day researchers of avian blood parasites, that in 1885 Danilewsky discovered *Plasmodium* in birds. At the time of his discovery he was experimenting with shrikes, jays and owls, all of which have since been shown to harbour malarial parasites. It is perhaps more significant, and not just a mere coincidence, that five years previous, Laveran described the causative agents of human malaria. Since that time the course of experimental observations with both types of parasites has proceeded side by side.

Early contributions in the field of avian blood parasites came from Russia, Germany, Italy, France, and shortly thereafter from North America. The earliest works were generated by the obvious implications of these parasites to human well being. Undoubtedly the importance of hematophagus Diptera to the medical entomologist has aided greatly in the development of our knowledge on the blood parasites of birds.

It was approximately thirteen years after the discovery of the endocorpuscular parasites of birds that serious consideration was given to this area of research in America. Scientists such as Opie (1898) published papers on the hematozoa and Sir Ronald Ross, in the same year, showed experimentally that malaria was transmitted by mosquitoes. Were it not for the use of birds as experimental hosts, it is doubtful whether the mosquito transmission of malaria would have been so clearly established.

The period from Ross up to 1923 was marked as a time of maximum species descriptions, with little work being conducted on the biology of the parasites. From that date to the present, numerous researchers have been involved and voluminous works produced with relation to the fields of avian parasitology and entomology. Hewitt (1940) suggests that over 75% of the papers on the subject of life cycles, etc., has appeared since 1923.

The earlier investigations relating to the blood parasites have been reviewed and summarized by Wenyon (1926). Since Wenyon's review much of the taxonomy of the blood parasites has been expanded and reported by authors such as Manwell (1935, 1938); Giovannola (1939); Hewitt (1940); Coradetti, Garnham and Laird (1963); Garnham (1966). (A point of interest mentioned by Bennett and Laird (1973) is that in many cases the creation of a new species of parasite is based on just a single blood film).

In addition to the reviews reported in the literature on the taxonomy of the parasites, there have also been a number of host lists prepared utilizing a wide variety of wild birds from many parts of the world. Among those which might be mentioned are: Wenyon (1926) - the most extensive; Coatney (1936, 1937); Coatney and Roudabush (1936, 1949); Herman (1944); Levine and Kantor (1959); Berson (1964); Hsu, Campbell and Levine (1973).

These latter surveys were useful in establishing the distribution of parasites in different hosts and aided much to our knowledge of geographic and host associations of the parasites in the hope of finding new forms. There have been several attempts to present infection rates and to interpret incidence or prevalence on the basis of the survey data, but according to Herman (1968), in many cases little significance can be placed on such interpretations because of the limited nature of the survey. This is particularly true in the case of small samples and the identification of parasites from single blood films.

The four groups of avian hematozoa that have captured much attention in previous and present investigations belong to the genera *Leucocytozoon*, *Haemoproteus*, *Plasmodium* and *Trypanosoma*. It has been shown in a number of cases, Bennett and Fallis (1960); Fallis and Bennett (1966); and Sherwood (1968) that these parasites can cause severe mortalities in young birds. Bennett *et al.* (1973) have summarized this aspect of the blood protozoans in birds.

Family Plasmodiidae

Plasmodium

Danilewsky's observation (1885) of *Plasmodium* in birds and the earlier discovery of the malaria pigments in human blood, provided the impetus for further work related to this particular avian parasite. Marchiafava and Celli (1889) proposed the generic name *Plasmodium* for the pigmented hematozoans which has maintained its priority to the present day. From the time of Grassi and Feletti (1890) it has been generally assumed that Danilewsky's parasite was the original discovery of *P. relictum*, but Garnham (1966) suggests that it may have been a parasite smaller than *P. relictum* that was actually concerned, possibly even *P. elongatum*.

From a taxonomic viewpoint, it must be made clear that the original descriptions were inadequate and in many cases the characteristics poorly represented. In 1892 Grassi and Feletti, recognizing the situation, prepared an extended paper in which seven species in the genus *Haemamoeba* (=*Plasmodium*) were described.

Better descriptions of the parasite followed in the remaining years of the century, but up to 1926, many workers followed Wenyon's thinking by grouping all malaria parasites under the name of *H. relicta*, or some other accepted synonym. Even in early years closely related species were often times grouped under this specific name.

Ronald Ross (1898) discovered that a mosquito (later identified as *Culex pipiens*) was the vector of *P. relictum*. These experiments which were carried out in India were based on feedings on infected sparrows and larks. In spite of the wide distribution of the parasite, and its ready transmissibility by domestic mosquitoes, the natural vector has rarely been identified.

Bruce Mayne (1928) in India was the first to recognize and point out the susceptibility of anopheline mosquitoes to bird malaria (*P. relictum*).

Family Leucocytozoidae

Leucocytozoon

The actual authorship of the genus *Leucocytozoon* has been an area of considerable controversy in recent years. Danilewsky, who first reported the parasite from the blood of owls in 1889, has for many researchers meant that he was also the original author. However, other workers of the time such as Berestnev, Ziemann and Sambon have also been attributed the honor by some present day researchers.

Bennett, Khan, Laird and Herman (in press) saw the need to assemble the pertinent literature and reassess the arguments concerning the authorship of the genus.

Bennett *et al.* in their paper "Remarks on the status of the genus *Leucocytozoon*" show very clearly that Danilewsky was claiming priority for the discovery and not the actual naming of the parasite. Furthermore, Danilewsky described and illustrated the parasite but he never "unequivocally" used the term *Leucocytozoon*.

In 1904 Berestnev coupled the generic and specific names to designate the parasites of owls, ravens and magpies as *L. danilewskyi*. Lühe (1906), although attributing the genus erroneously to Denilewsky, presented the first formal description of it. Bennett *et al.* (in press) propose that this designation be retained and the genus properly ascribed to Lühe. Lühe's description and those of several researchers shortly afterward have all referred *Haemamoeba majoris* to *Leucocytozoon*. It is thus suggested that the first species *Leucocytozoon* (=*Haemamoeba*) *majoris* becomes the type species of the genus, replacing *L. danilewskyi*. In 1965, Bennett *et al.* redefined the genus and created the genus *Akiba* to receive *Leucocytozoon caulleryi*. The separation of the genera was based on clearly defined morphological characteristics in vertebrate and invertebrate hosts.

The transmission of *Leucocytozoon* by simuliids was first reported by O'Roke (1934). His account demonstrated the transmission of *L. anatis* (=*simondi*) in *Simulium venustum*. (It is likely that he failed to recognize *S. rugglesi*.) Since that time various species of ornithophilic blackflies have been clearly demonstrated to be the natural vectors of this parasite, e.g. Fallis and Bennett (1958).

Family Haemoproteidae

Haemoproteus (Parahaemoproteus)

In the same year as Danilewsky first noted *Leucocytozoon*, Kruse (1890) was responsible for giving the name *Haemoproteus* to an ill-defined, poorly-described parasite for which he stated no host. The name was given page priority over *Halteridium* (Labbe, 1894), a much more adequately described and descriptive term for the crescent shaped bodies first noted by Danilewsky.

Following that date, numerous species of *Haemoproteus* have been named in birds, more on the basis of their discovery in a certain avian host than on any morphological features. As a result several so-called species of *Plasmodium* are now recognized as belonging to the family Haemoproteidae, e.g. *H. centropi* and *H. gallinulae* of Indian birds (de Mello, 1935).

Bennett *et al.* (1965) recognized two genera of hemoproteids particularly common in birds and proposed the division of the genus into two, namely *Haemoproteus* and *Parahaemoproteus*. They designated *Haemoproteus* as the type genus with the type species as *H. columbae* Celli and Sanfelice, (1891) and *P. canachites* Fallis and Bennett (1960) as the type species of *Parahaemoproteus*.

The active transmission of *Haemoproteus* by hippoboscids (louse flies) is well substantiated in the literature by authors such as Adie (1924) and Aragao (1919) working with *H. columbae* and Baker (1963) with English Wood Pigeons. However, Fallis and Wood (1957) and Fallis and Bennett (1960) showed that the sporogony of others is completed in *Culicoides* spp. Bennett *et al.* (1965) point out that although hippoboscids have been implicated as hosts for at least three species of *Haemoproteus*, many of the other species occur in birds which do not harbour hippoboscids. These have been shown to be transmitted by *Culicoides* and to be members of the genus *Parahaemoproteus* e.g. *P. nettionis*, *P. canachites* and *P. fringillae*.

Family Trypanosomatidae

Trypanosoma

The history of various aspects of our knowledge of trypanosomes has been dealt with by a number of authors: Laveran and Mesnil (1912); Wenyon (1926); Cole (1926); Scott (1939); Curasson (1943); and others.

From these reports it appears that the first trypanosome was observed nearly 300 years ago by Antony van Leeuwenhoek, the Father of Protozoology. In 1680 he described organisms, seen by him, in the gut of horseflies (Tabanidae) which might have been the development stages of the bovine trypanosome, *T. theileri*.

In 1841, Valentin, a Professor of Physiology, at the University of Berne described the finding in the blood of trout (*Salmo fario*) of motile elongated organisms which he likened to amoebae. However, the true nature was uncertain.

Gruby (1843), a Hungarian who eventually settled in Paris, was the first to recognize the true nature of the batrachian parasites.

For these hemoflagellates which were seen by his predecessors and himself, he created the generic name *Trypanosoma*.

The first satisfactory account of trypanosomes in birds was that of Danilewsky (1885), who named the species *T. avium*. Since that time a large number of forms have been described. However, as with the other hemoprotozoans, in many cases little more has been done than to give an account of the trypanosomes as they appeared in a single blood film.

Information relating to the transmission of *Trypanosoma* is more difficult to interpret than those of the other described blood parasites (Bennett, 1960). Baker (1956) demonstrated the transmission of *T. avium* by the hippoboscid *Ornithomyia avicularia* and Grewal and Chowdhary (1957) illustrated its transmission by mosquitoes. Duke and Robertson (1912) suggested simuliids as vectors of avian trypanosomes in Uganda.

In Algonquin Park, Bennett (1961) showed that the flagellates will develop in and can be transmitted by black flies, biting midges, and mosquitoes.

PART I

(NORTH AMERICAN STUDY)

INTRODUCTION

This portion of the thesis was conducted to analyse in detail the prevalence of *Leucocytozoon, Haemoproteus* and *Plasmodium* in birds of North America. The prevalence of the various species of blood protozoa is studied in relation to the breeding behavior of the birds along with the known feeding behavior of the vectors of the avian hematozoa.

Members of *Leucocytozoon* have been shown to be transmitted in North America by simuliids (O'Roke, 1934; Fallis, Anderson and Bennett, 1956; Fallis and Bennett, 1958; Bennett and Fallis, 1960). Similarly, some simuliids have been shown to exhibit strong host specificity (Bennett, 1960; Fallis and Smith, 1964; Lowther and Wood, 1964). This is particularly significant when the incidence of the parasite is considered in relation to the occurrence of their probable vectors.

Haemoproteus (*Parahaemoproteus*) is reported to be transmitted in North America by *Culicoides*, (Fallis, Anderson and Bennett, 1956; Fallis and Bennett, 1958; Fallis and Wood, 1957; Fallis and Bennett, 1960). As is the case with *Leucocytozoon*, host specificity has been indicated for *Haemoproteus*. Fallis and Bennett, (1960) showed that a specificity for grouse is clearly apparent for *Haemoproteus* (*Parahaemoproteus*) *canachites*. Other reports have also indicated the presence of species in one type of bird and not in others.

Plasmodium, although transmitted by mosquitoes, is virtually unknown with regard to host specificity. This is partly attributed to the difficulty in obtaining blood fed mosquitoes in quantitatively significant numbers to draw any conclusions. Bennett's study (1960) in Algonquin Park, noted the occurrence of many mosquito species but that few were captured following engorgement on birds.

It is felt in view of published literature on the topic, that a study of North American birds will elucidate the premise that birds acquire their infections on the breeding ground, (Bennett and Laird, 1973).

MATERIALS AND METHODS

The WHO International Reference Center for Avian Malaria Parasites at the Department of Biology, Memorial University of Newfoundland, St. John's, currently holds information pertaining to approximately 35,000 bird blood smears. The data is recorded on a punch-card system which utilizes a multiple sorting code, permitting the retrieval of information under a number of headings.

The abstraction of the data on North American birds from the system was time consuming and had to be carried out in several steps. Initially the information required was a compiled list of all the birds from North America which have been recorded by the WHO Center. Following this major breakdown the birds were separated into several categories to facilitate a more relevant and comprehensive study of the host-parasite problem in this section of the globe. The major categories were: 1. Bird Families 2. Bird Species 3. Overall Parasite prevalence for each of the bird families 4. The specific parasite prevalence for each of the bird species.

The above data is reported in Table I and constitutes the main source of reference for further discussion in this section. The author has seen fit to entitle this section, "UNSTRATIFIED", as it represents the unaltered material initially reported by the original researcher. Its importance or significance lies in the fact that it presents an overall picture of the avian blood problem in North America. This is particularly true in as far as these

TABLE I

Prevalence of hematozoa in North American birds. Due to multiple infections, total infections by parasite species are greater than the total number of infected birds. Hematozoan infections are represented as percents of infected birds. "Others" ( ) are expressed as numbers and were either trypanosomes or microfilaria. The underlined strata denotes preferred habitat of bird.

Bird and Family	Strata	Total Birds	Total Positive	Percent Positive	% Leucocytozoon	% Haemoproteus	% Plasmodium	Others
ACCIPITRIDAE								
Accipiter cooperii	4	1	1	100.0	100.0			
Accipiter striatus	3,4	12	8	66.6	100.0			
Accipiter gentilis	4,5	1						
Circus cyaneus	1,5	4						
Pandion haliaetus	1,2,3,4	1						
Buteo lineatus	4	2	2	100.0	50.0			(1)
Total:		21	11	52.4	100.0			(1)
AEGITHILIDAE								
Psaltriparus minimus	2,3	2						
Total:		2						
ALAUDIDAE								
Eremophila alpestris	1	5	2	40.0		100.0		
Total:		5	2	40.0		100.0		
ARDEIDAE								
Botaurus lentiginosus	5	8						
Butorides virescens	3,4	3						
Ixobrychus exilis	6	1						
Casmerodius albus	2,3,4	2						
Total:		14						

TABLE I (continued)

Bird and Family	Strata	Total Birds	Total Positive	Percent Positive	% *Leucocytozoon*	% *Haemoproteus*	% *Plasmodium*	Others
ANATIDAE								
Anas carolinensis	5	279	122	43.7	33.6	59.0	22.1	
Anas discors	5	698	64	9.2	46.9	35.9	23.4	
Anas platyrhynchos	5	450	177	39.3	15.3	62.7	24.3	
Anas rubripes	5	875	719	82.2	39.4	72.9	18.6	
Aix sponsa	5	594	491	82.7	19.3	91.9	21.0	
Anser albifrons	5	5	1	20.0	100.0			
Aythya americana	5	30	2	6.7	100.0			
Aythya collaris	5	119	25	21.0	20.0	72.0	20.0	
Branta canadensis	5	305	17	5.6	82.4	29.4	5.9	
Chen caerulescens	5	694	21	3.0	76.2	4.8	9.5	
Aythya marila	5	3	1	33.3				(1)
Clangula hyemalis	5	2	2	100.0		50.0		(1)
Melanitta perspicillata	5	5	3	60.0	66.6	33.3		
Mergus serrator	5	7	5	71.4	80.0	20.0		
Mareca americana	5	161	37	23.0	2.7	75.7	43.2	
Anas acuta	5	120	51	42.5	45.0	43.1	25.5	
Anser anser	5	112	109	97.3	96.3			(4)
Oidemia nigra	1,5	2	2	100.0	50.0	50.0		
Total:		4461	1849	41.4	35.2	68.1	19.4	
BOMBYCILLIDAE								
Bombycilla cedrorum	2,3,4	14	8	57.1	75.0			(2)
Total:		14	8	57.1	75.0			

TABLE I (continued)

Bird and Family	Strata	Total Birds	Total Positive	Percent Positive	% Leuco-cytozoon	% Haemo-proteus	% Plas-modium	Others
CERTHIDAE								
Certhia familiaris	2,<u>3</u>	4	1	25.0	100.0			
Total:		4	1	25.0	100.0			
CHARADRIIDAE								
Arenaria melanocephala	1	3						
Arenaria interpres	1	1						
Charadrius alexandrinus	1	3						
Charadrius vociferus	1	1	1	100.0				(1)
Charadrius semipalmatus	1	4						
Squatarola squatarola	1	1						
Total:		13	1	7.7				
CATHARTIDAE								
Cathartes aura	1	1	1	100.0				(1)
Total:		1	1	100.0				
CHAEMAIDAE								
Chamaea fasciata	2	1	1	100.0				(1)
Total:		1	1	100.0				

TABLE I (continued)

Bird and Family	Strata	Total Birds	Total Positive	Percent Positive	% Leucocytozoon	% Haemoproteus	% Plasmodium	Others
COLUMBIDAE								
Columba fasciata	3	3	2	66.6	50.0		50.0	
Columba livia	3	8	8	100.0		75.0	25.0	
Zenaida macroura	3	84	84	100.0	13.0	80.9	7.1	
Zenaida asiatica	3	4	4	100.0		100.0		
Total:		99	98	99.0	12.2	79.6	9.2	
COLYMBIDAE								
Podilymbus podiceps	5	3						
Total:		3						
CORVIDAE								
Perisoreus canadensis	2	42	11	26.2	45.5	18.2	9.0	(3)
Corvus brachyrhynchos	2,3,4	9	1	11.1		100.0		
Cyanocitta cristata	2	34	21	61.8	81.0	61.9		
Total:		85	33	38.8	66.6	48.5	3.0	
FALCONIDAE								
Falco sparverius	3	5	1	20.0	100.0			
Total:		5	1	20.0	100.0			

TABLE I (continued)

Bird and Family	Strata	Total Birds	Total Positive	Percent Positive	% Leuco-cytozoon	% Haemo-proteus	% Plas-modium	Others
FRINGILLIDAE								
Acanthis flammea	1,2,3,4	9	6	66.6	50.0	66.6		
Carpodacus purpureus	2,3,4	79	68	86.0	85.3	41.2	1.5	
Carpodacus mexicanus	2	1290	833	64.6	10.7	23.3	72.9	
Chondestes grammacus	2	194	194	100.0	0.5	81.4	8.2	
Junco hyemalis	1	71	38	53.5	73.7	50.0		
Junco oreganus	1	7	6	85.7	16.7	83.3	50.0	
Melospiza lincolnii	1,5	16	10	62.5	90.0	50.0		
Melospiza georgiana	2	115	100	87.0	93.0	47.0		
Melospiza melodia	2	99	37	37.4	64.9	21.6	10.8	
Passerculus sandwichensis	1	40	21	52.5	71.4	95.2	4.8	
Passerella iliaca	1,2	397	326	82.1	90.5	47.9	1.2	
Passerina amoena	2	12	9	75.0	77.8	33.3		
Pipilo erythrophthalmus	1	26	12	46.2	8.3	33.3	50.0	(1)
Pooecetes gramineus	1	3	2	66.6	50.0	50.0		
Pinicola enucleator	2,3	50	50	100.0	78.0	76.0		
Pheucticus melanocephalus	2,4	67	55	82.1	49.1	67.3	1.8	
Spizella arborea	3	19	15	78.9	100.0	40.0		
Zonotrichia albicollis	1,2,3	250	192	76.8	67.7	61.5	2.1	
Zonotrichia leucophrys	1,2,3	208	206	99.0	43.7	63.6	5.3	
Spizella passerina	3	27	22	81.5	63.6	36.4		
Loxia leucoptera	2,3	13	7	53.8	71.4	42.9		
Loxia curvirostra	2,3	7	4	57.1	100.0	50.0		
Cardinalis cardinalis	2	5	5	100.0				(5)
Total:		3004	2218	73.8	42.8	44.9	29.7	

TABLE I (continued)

Bird and Family	Strata	Total Birds	Total Positive	Percent Positive	% Leucocytozoon	% Haemoproteus	% Plasmodium	Others
GRUIDAE								
Grus canadensis	5	2	2	100.0	50.0	100.0		
Total:		2	2	100.0	50.0	100.0		
HIRUNDINIDAE								
Hirundo rustica	3	71	5	7.0	20.0			(4)
Iridoprocne bicolor	3	1	1	100.0	100.0			
Total:		72	6	8.3	33.3			
ICTERIDAE								
Agelaius phoeniceus	6	708	97	13.7	28.9	24.7	14.4	
Euphagus cyanocephalus	2	150	85	56.6	4.7	28.2	34.1	
Euphagus carolinus	5	18	18	100.0	94.4			
Icterus bullockii	2,3	634	634	100.0	1.3	94.3	10.1	
Quiscalus quiscula	1-6	98	65	66.3	80.0	12.1		(5)
Sturnella neglecta	1	2	1	50.0			100.0	
Xanthocephalus xanthocephalus	6	23	23	100.0			91.3	(2)
Total:		1633	923	56.5	12.0	70.7	14.0	
MIMIDAE								
Dumetella carolinensis	2	42	8	19.0			12.5	(7)
Mimus polyglottus	2	67	20	29.8	25.0		60.0	(3)
Total:		109	28	25.7	17.8		46.4	

TABLE I (continued)

Bird and Family	Strata	Total Birds	Total Positive	Percent Positive	% Leucocytozoon	% Haemoproteus	% Plasmodium	Others
PARIDAE								
Parus atricapillus	2	83	66	79.5	95.4	4.5	3.0	
Parus hudsonicus	2	93	44	47.3	72.7	6.8		(9)
Total:		176	110	62.5	86.4	5.5	1.8	
PARULIDAE								
Dendroica auduboni	2	45	14	31.1	50.0	21.4		(4)
Dendroica caerulescens	2,4	9	2	22.2	50.0			(1)
Dendroica coronata	3	101	65	64.3	78.5	46.2		
Dendroica castanea	2	27	13	48.1	69.2	30.8		
Dendroica fusca	2,3,4	12	5	41.6	100.0	80.0		
Dendroica pensylvanica	1,2	6	5	83.3	20.0			(4)
Dendroica petechia	2	74	54	72.9	96.3	11.1	1.8	
Dendroica pinus	3	27	22	81.5	90.9	22.7		
Dendroica palmarum	3	2	2	100.0	100.0			
Dendroica striata	3	276	238	86.2	87.8	40.8	3.4	
Dendroica virens	2	11	4	36.4	100.0			
Dendroica tigrina	5	6	4	66.6	25.0		25.0	(2)
Mniotilta varia	1,2	60	32	53.3	84.4	3.1		(4)
Oporornis philadelphia	1,2	20	13	65.0	100.0			
Geothlypis trichas	1,2	32	11	34.4	18.2			
Seiurus aurocapillus	1	87	10	11.5	70.0			(3)
Seiurus novaboracensis	1	359	261	72.7	93.5	33.0	2.3	
Setophaga ruticilla	2,3	30	10	33.3	80.0			(2)
Vermivora celata	1,2	6	1	16.6	100.0			
Vermivora peregrina	1,2	59	18	30.5	83.3	5.6		(2)
Vermivora ruficapilla	1,2	90	26	28.8	80.8			(5)

TABLE I (continued)

Bird and Family	Strata	Total Birds	Total Positive	Percent Positive	% Leuco-cytozoon	% Haemo-proteus	% Plas-modium	Others
PARULIDAE								
Wilsonia canadensis	1,6	36	13	27.6	53.8			(6)
Wilsonia pusilla	2,5	154	106	68.8	95.3	1.9	1.9	(1)
Total		1529	929	60.8	87.0	25.7	1.9	
PHASIANIDAE								
Lophortyx californica	1	53	24	45.3		95.8		
Total:		53	24	45.3		95.8		
PLOCEIDAE								
Passer domesticus	2,3,4	549	509	92.7		1.6	60.7	
Total:		549	509	92.7		1.6	60.7	
PICIDAE								
Colaptes auratus	2,3,4	34	30	88.2	23.3	93.3		
Colaptes cafer	2,3,4	2	2	100.0			100.0	
Dendrocopus villosus	2,3,4	24	15	62.4	13.3	100.0		
Dendrocopus pubescens	2,3,4	25	4	16.0		100.0		
Picoides arcticus	2,3	5	2	40.0		100.0		
Sphyrapicus varius	2,3,4	6	4	66.6		100.0		
Total:		96	57	59.4	15.8	93.0		

TABLE I (continued)

Bird and Family	Strata	Total Birds	Total Positive	Percent Positive	% Leucocytozoon	% Haemoproteus	% Plasmodium	Others
RALLIDAE								
Fulica americana	5	4						
Gallinula chloropus	5	4						
Total:		8						
SCOLOPACIDAE								
Actitis macularia	1	1						
Capella gallinago	1,5	64						
Catoptrophorus semipalmatus	1	3						
Calidris canutus	1	2						
Erolia minutilla	1	2						
Ereunetes mauri	1	2						
Erolia fuscicollis	1	1						
Numenius americanus	1	1						
Numenius phaeopus	1	2						
Limosa fedoa	1	4						
Limnodromus griseus	1	9	8	88.8	25.0	25.0		(4)
Tringa flavipes	1	1						
Tringa solitaria	3,4	2						
Philohela minor	1	43						
Total:		137	8	5.8	25.0	25.0		
SITTIDAE								
Sitta carolinensis	2,3,4	3						
Sitta canadensis	2,3,4	5						
Total:		8						

TABLE I (continued)

Bird and Family	Strata	Total Birds	Total Positive	Percent Positive	% Leuco-cytozoon	% Haemo-proteus	% Plas-modium	Others
STRIGIDAE								
Aegolius acadicus	3,4	18	18	100.0	100.0			
Aegolius funereus	3,4	9						
Micrathene whitneyi	3	1						
Otus asio	3,4	1						
Total:		29	18	62.0	100.0			
STURNIDAE								
Sturnus vulgaris	3,4	21						
Total:		21						
SYLVIIDAE								
Regulus calendula	3,4	37						
Regulus satrapa	3,4	3						
Total:		40						
TETRAONIDAE								
Bonasa umbellus	1	309	169	54.6	60.9	21.9	4.7	
Canachites canadensis	1	93	46	49.4	37.0	17.4		
Dendragapus obscurus	1	612	249	40.6	36.9	57.0	30.9	
Lagopus lagopus	1	354	171	48.3	92.4	1.8		
Total:		1,368	635	46.4	58.3	30.0	13.4	

TABLE I (continued)

Bird and Family	Strata	Total Birds	Total Positive	Percent Positive	% Leucocytozoon	% Haemoproteus	% Plasmodium	Others
THRAUPIDAE								
Piranga olivacea	2,3,4	8						
Piranga ludoviciana	2,3,4	20	16	80.0	12.5	81.3	6.3	
Total:		28	16	57.1	12.5	81.3	6.3	
TURDIDAE								
Catharus guttatus	1	19	10	52.6	100.0			
Catharus fuscescens	1	19	10	52.6	70.0			
Catharus minimus	1	156	122	78.2	93.4	22.1	0.8	
Catharus ustulatus	1	156	118	75.6	30.5	0.8		
Turdus migratorius	1-6(2)	228	165	72.3	95.2	38.8	4.2	
Total:		578	425	73.5	76.2	21.6	1.8	
TYRANNIDAE								
Empidonax flaviventris	1	115	28	24.3	50.0	10.7		
Total:		115	28	24.3	50.0	10.7		
VIREONIDAE								
Vireo flavifrons	2							
Vireo olivaceus	2	72	41	56.9	56.0	39.0		
Vireo philadelphicus	2	2						
Vireo solitarius	3	3	1	33.3	100.0			
Total:		77	42	54.5	57.1	38.1		
OVERALL TOTAL:		14,360	7,984	55.6	43.0	45.7	20.0	

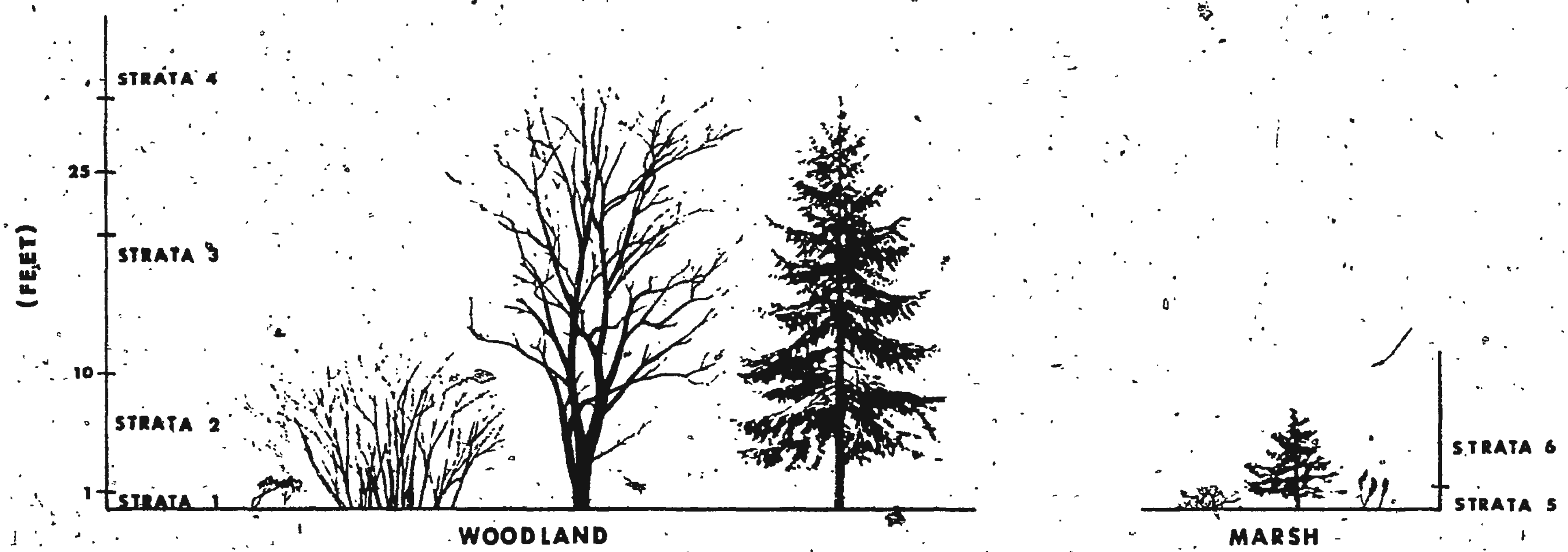
slides represent a large sample over a wide geographic area of North America.

The other major division under which the North American material is studied has been identified as "STRATIFIED". In this section, the data presented is based on a system of habitat preferences for the host as designed by the author (Figure 1). The system was developed, following an examination of other systems which have been used along similar lines and an extensive perusal of the ornithological literature (particularly Bent, 1963 *et. seq.*) to determine the nesting sites and most commonly utilized habitats by the various bird groups.

Following the establishment of the "Stratification System" the data on numbers of birds, parasite prevalence, etc., previously established in Table I, were compiled and assigned its particular stratum. The results of this compilation are reported in Table III and constitute the major source of reference for the "Stratified" portion of the North American study.

Figure 1.

Stratification system utilized in determining preferred habitats of North American birds.


STRATA 4
STRATA 3
STRATA 2
STRATA 1
(FEET)
25
10
1
WOODLAND
MARSH
STRATA 6
STRATA 5

RESULTS AND DISCUSSION

UNSTRATIFIED

The data presented in Table I represents one of the largest samplings of terrestrial birds studied collectively on North American blood parasites. The 37 families and 163 species comprising the list gives a cross-section of the various bird groups resident on the North American Continent compared with an approximate total of 760 species of approximately 65 families.

Prior to this study, one of the first extensive studies in this part of the world was carried out on ducks in Michigan by O'Roke (1934). The first real extensive survey on a variety of wild birds was undertaken by Herman (1935) in which he examined 652 birds in the Syracuse, N.Y. region. Wirth (1944) reported the incidence of blood parasites in nature as reported by workers in the United States up to that time. His work involved approximately 4750 birds. Bennett and Fallis (1960) reported the incidence of blood parasites in birds in Algonquin Park over a period of 13 years from 1947-1959. The total birds examined in that study was 3004.

Numerous other studies have been reported from time to time and from many parts of the world. The emphasis, however lies in the temperate parts of the world, which according to Herman (1968) is accounted for by the fact that there are a greater abundance of investigators in these areas. As often is the case, the geographic separation of these surveys has the effect of making data incomparable. Another factor which limits the value of all surveys is the relatively small samplings, thus resulting in negative findings, or giving insufficient data for significant comparisons.

The overall infection rate of 55.6% reported in Table I is an interesting one and deserves some further comment.

Wirth (1944) reported an incidence of blood parasites in his study as 13.7%. Huff (1932) reported a parasite incidence of 27% amongst a total of 967 birds. A study, in some ways similar to the present one, conducted in Algonquin Park (Bennett and Fallis, 1960) shows an infection rate of 49%. Wood and Herman (1942) reports 48.2% infection in 1,525 birds covering 112 sp. In reviewing the blood smears harboured at the WHO Center at Memorial University of Newfoundland, Bennett and Laird (1973) established that 72% of the birds had one or more parasites. A further survey conducted by Bennett (1972) on the birds of Labrador reports a 60% infection level for the Churchill Falls region and 28% for the Goose Bay area. Passeriform birds of insular Newfoundland (Bennett and Laird, 1973) are shown to have an overall infection rate of 80 - 90%.

Although the levels of infections reported vary over quite an extensive range, it does give strength to the idea that North America does have a significant avian blood parasite problem. Whether or not the statistic detailed in Table I or those cited above are true indications of the overall problem will only be answered following more testing using larger sample sizes.

The specific parasite infections (Table I) shows a relatively small difference between the *Leucocytozoon* and *Haemoproteus* prevalence in the infected birds (43% compared with 45.7%). The figure (20%) given for *Plasmodium* would appear to be reasonably sound and generally accepted in light of other published reports. Bennett and Fallis (1960) report 18.2% *Plasmodium* infection while Wood and Herman (1942) gives the figure of 19.9% infection.

The *Leucocytozoon* and *Haemoproteus* infections, as determined from the literature, are not as consistent in their reporting. Bennett and Fallis (1960) shows the incidence of *Leucocytozoon* as approximately 64% when compared with only 25.8% of the birds having a *Haemoproteus* infection. Wood and Herman (1942) reported 44.5% of the infected birds had *Haemoproteus* and *Leucocytozoon* accounted for 34.4%. Bennett, Campbell, Cameron (in press) noted that 92% of the infected Newfoundland passeriform birds possessed species of *Leucocytozoon* whereas only 37.5% harboured *Haemoproteus*.

Huff (1932) points out that the most common parasite of birds belong to the genus *Haemoproteus*. Herman (1963) states that *Leucocytozoon* appears to be the most important parasite in the Anatidae. It is also a widely accepted fact by workers in the field that *Haemoproteus* is a common parasite of the Columbiformes particularly *Columba livia*, California quail, ducks and grouse. From these few examples it would appear that an attempt at establishing common parasites of specific birds or bird groups represents a monumental task, at least with these two major parasitic protozoa. Many additional factors, such as availability of vectors, suitable climatic conditions and details of the local environmental situation are instrumental in the eventual production of answers regarding this problem.

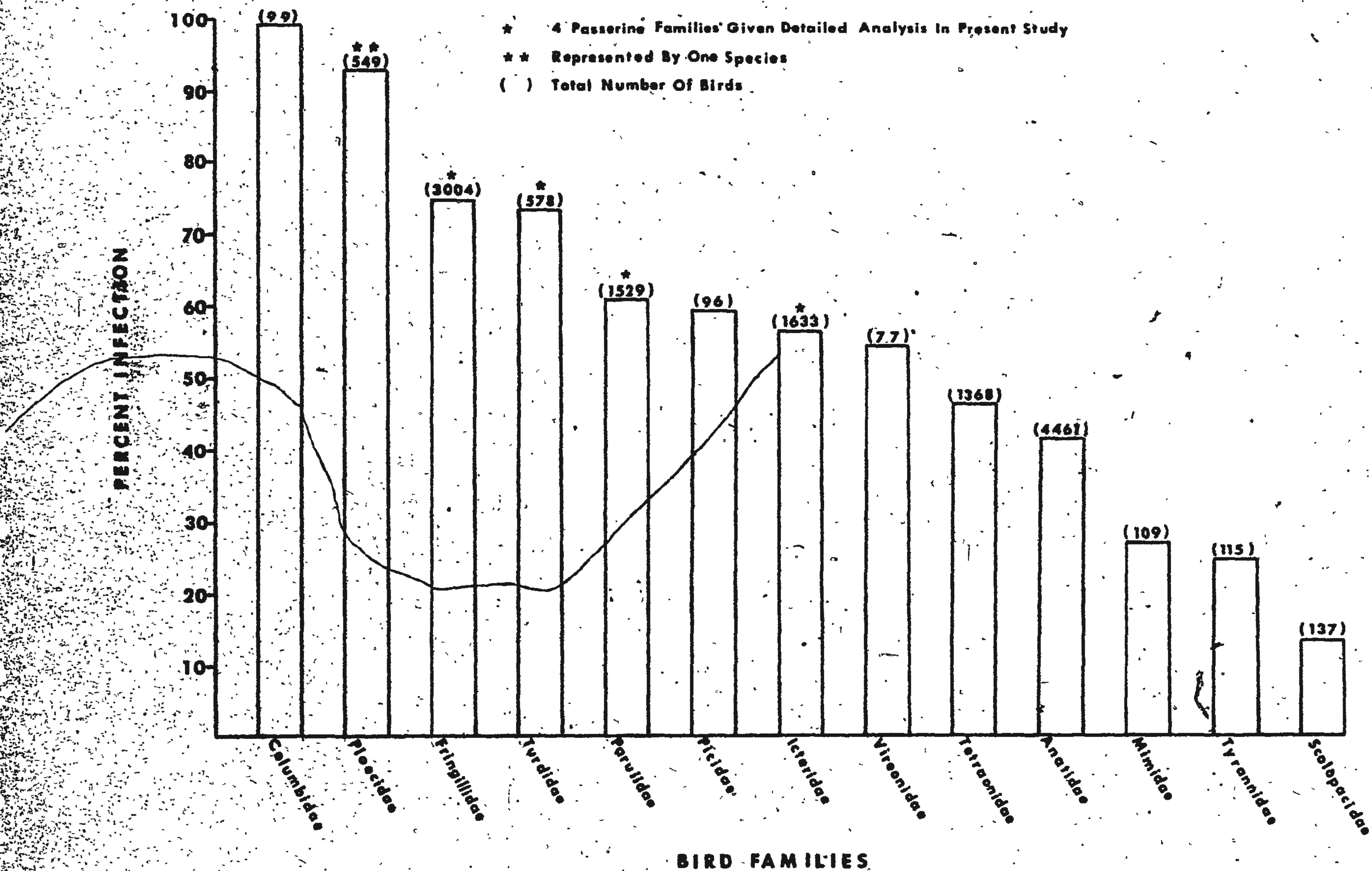
It is apparent (Table I) that certain families are not only more susceptible to infection than others, but also more prone to specific parasite infections. This point is particularly true when the families represented by reasonably large sample sizes are considered (Figure 2). The bar diagram illustrates that the major Passerine families, Fringillidae, Icteridae, Parulidae and Turdidae, are highly susceptible families for the avian hematozoa. The Ploceidae and Columbidae are not considered at this time because the total number of birds reported for these groups comprises a small number of species.

The prevalence of the specific parasites (Figure 3) is presented for the six major bird families under study. These bird groups are considered as "major", in that they represent 87.5% of the total birds examined.

The Fringillidae are observed as being fairly consistent in its *Haemoproteus* (44.8%) and *Leucocytozoon* (42.8%) infections

Figure 2.

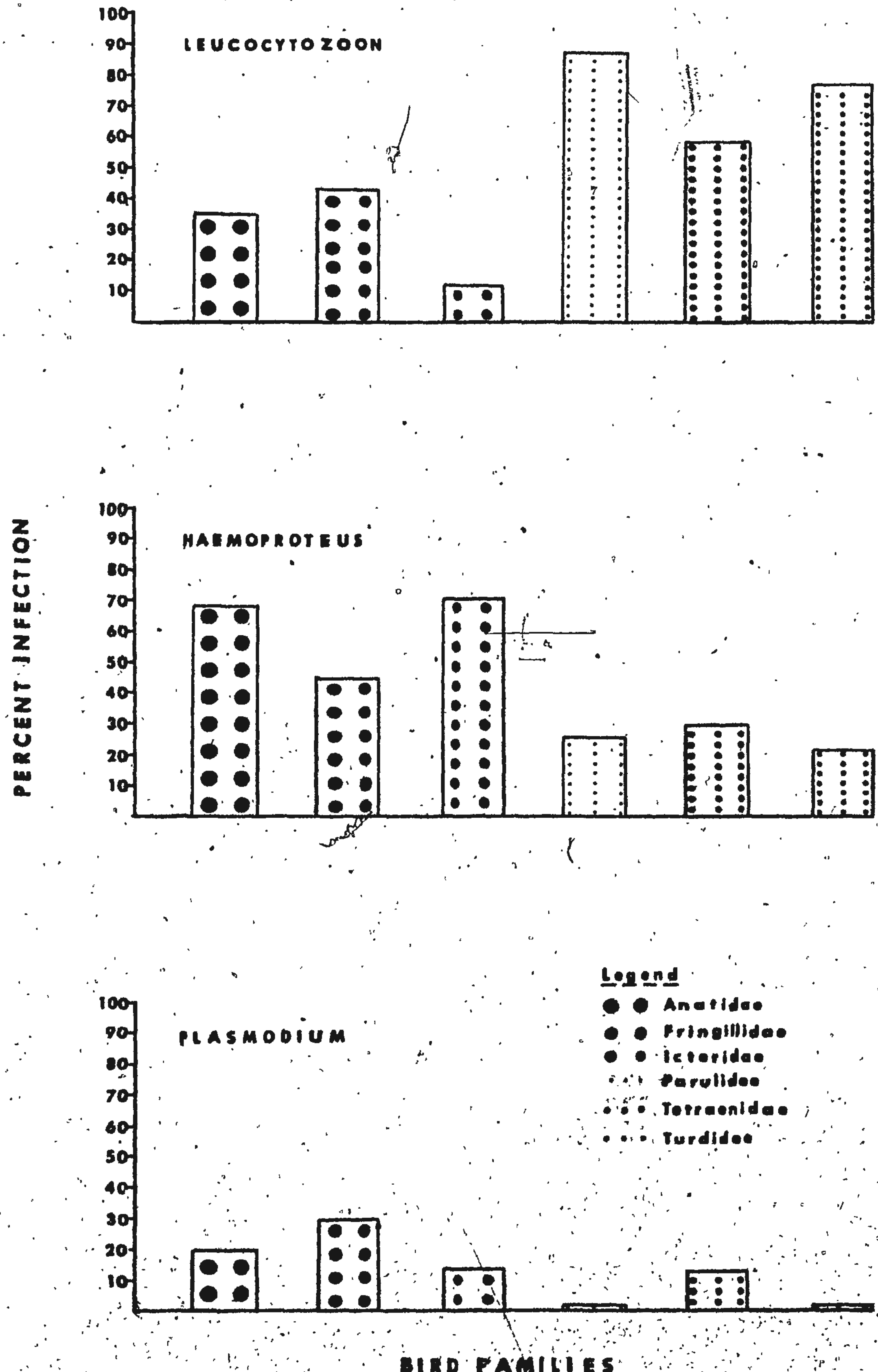
Parasite prevalence of the major bird families contributing to the North American bird survey.



* 4 Passerine Families Given Detailed Analysis In Present Study
** Represented By One Species
( ) Total Number Of Birds
PERCENT INFECTION
100
90
80
70
60
50
40
30
20
10
(99)
** (549)
* (3004)
* (578)
* (1529)
(96)
* (1633)
(77)
(1368)
(4461)
(109)
(115)
(137)
Columbidae
Ploceidae
Fringillidae
Turdidae
Parulidae
Picidae
Icteridae
Vireonidae
Tetraonidae
Anatidae
Mimidae
Tyrannidae
Scolopacidae
BIRD FAMILIES

Figure 3.

A comparison of prevalence of
Leucocytozoon, *Haemoproteus* and *Plasmodium*
in six bird families:
Anatidae, Fringillidae, Icteridae, Parulidae, Tetraonidae and Turdidae



LEUCOCYTOZOON
HAEMOPROTEUS
PLASMODIUM
PERCENT INFECTION
100
90
80
70
60
50
40
30
20
10
Legend
Anatidae
Fringillidae
Icteridae
Parulidae
Tetraenidae
Turdidae
BIRD FAMILIES

as well as possessing the highest rate of *Plasmodium* infection. The Anatids, Icterids and Fringillids are collectively responsible for approximately 80% of the total *Haemoproteus* infection. Similarly, the major percentage of the *Leucocytozoon* infection is concentrated in four families namely, Parulidae, Turdidae, Tetraonidae and Fringillidae.

A closer examination of Table I shows that within particular bird families the parasite prevalence varies from species to species. In the Icteridae, for example, *Agelaius phoeniceus* represented by a total of 708 birds, had an infection rate of only 13.7% whereas, 643 *Icterus bullockii* had a parasite prevalence of 100%. More significant than the overall prevalence in the latter species is the point that 94.3% of the infected birds harboured *Leucocytozoon*.

Similar findings are noted within most of the bird families, i.e. specific parasites were more common in some species and not in others. For example, 72.9% of the infected *Carpodacus purpureus* harboured *Plasmodium*, whereas the remainder of the Fringillidae possessed very low levels of the parasite and in a number of cases it was completely absent. Generally the Parulidae exhibit a high level of *Leucocytozoon*, with the other two hematozoan species being relatively scarce. Species of *Haemoproteus* were especially common in the woodpeckers, some sparrows, blackbirds and ducks, but rare or absent in the Paridae, warblers, geese and flycatchers. The four Passerine families are observed (Figure 2) to have an infection rate which is markedly higher than that of the overall average (Table II) and greater than the six families taken collectively, as described previously. On the basis of these observations, much of the specific data in the stratified portion of the North American study has been designed around the four Passeriform families, i.e. Fringillidae, Icteridae, Parulidae and Turdidae.

TABLE II

Comparison of total birds and parasite prevalence in three different bird groupings.

	Total Birds	Total Positive	Percent Positive	* % Leucocytozoon	* % Haemoproteus	* % Plasmodium
Total of 4 Passerine Families (Fig.2)	6730	4495	66.8	49.3	44.0	18.1
Total of 6 Families (Fig.3)	12559	6979	55.6	46.0	49.1	18.0
Total Families as per Table I	14360	7984	55.6	43.0	45.7	15.9

*Infection rates presented are percents of infected (positive) birds.

STRATIFIED

The birds presented in Table I are known to vary in their habitats and nesting sites. This fact, along with the apparent differences in the rates of infection and parasite prevalence, forms the basis for this portion of the North American results. With these two points in mind, a stratification system was designed (Figure 1) in an attempt to place the birds in their most susceptible location for infection within the woodland and marsh environments.

Habitat selection is presented (Figure 1) as a function of vertical stratification in the woodland (coniferous and deciduous) and marsh environments. Strata 1 is intended to include all birds which normally nest at the ground level in the woodland environment. Thus the designation (0-1 ft.) would include the ground cover and low bushes found at this level. Strata 2 (2-10 ft.) takes in the level which is usually occupied by birds nesting in the shrubs and low tree levels up to 10 ft. Strata 3 includes the mid canopy levels (11-25 ft.) in the forest environment. Strata 4 is designated as the top canopy (25 ft. and upward) and would include those birds which frequently nest in the tree tops.

Strata 5 and 6 are assigned to the marsh environment and can be considered as equivalent to Strata 1 and 2 of the woodland environment in as far as the vertical stratification is concerned. Specifically, Strata 5 represents the area in which birds are found nesting in the low bushes on the marsh surface. Similarly, Strata 6 would include the shrub habitat beside water in the marsh environment.

The system was conceived after much study of the nesting sites and habitats frequented by the bird groups as reported in the literature by Bent (1963) and Godfrey (1966). Personal communication with Bennett and Herman and a perusal of a similar system used by Bennett (1957) in his study on the genus *Protocalliphora* were of tremendous help in the final construction of the system.

Although this system can be criticized for its breakdown, where various birds tend to overlap in more than one level, it is felt that in the main, the model can be substantiated by literature reports and field observations. Its primary function lies in the fact that it does provide a framework within which the avian blood parasite problem can be studied systematically. The implications of this type of approach must ultimately be considered in the light of the feeding behavior and habitats of the vectors. (This latter point is expanded in the Newfoundland Section of Results.)

Each of the species fitting a particular stratum was grouped (according to Figure 1) with other members of its family at its preferred level and presented in Table III. This approach enables the study of nesting sites (assumed to be critical locations for infection) of the birds as well as the distribution of the parasite prevalence throughout its natural habitat. In situations where birds were reported to nest in several strata, the one selected represents the preferred habitat as determined from literature reports and direct observations made by ornithologists in the field.

TABLE III

Parasite prevalence of North American bird families utilizing the strata system.

Strata	Family	Total Birds	Total Positive	Percent Positive	% Leuco-cytozoon	% Haemo-proteus	% Plas-modium	Others
1	ACCIPITRIDAE	4						
	ALAUDIDAE	5	2	40.0		100.0		(1)
	CHARADRIIDAE	13	1	7.7				(1)
	CATHARTIDAE	1	1	100.0				(1)
	FRINGILLIDAE	1004	813	81.0	70.0	56.5	3.6	
	ICTERIDAE	2	1	50.0			100.0	
	PARULIDAE	482	284	58.9	90.8	30.3	2.1	(9)
	PHASIANIDAE	53	24	45.3		95.8		(1)
	SCOLOPACIDAE	135	8	5.9	25.0	25.0		(4)
	TETRAONIDAE	1368	635	46.4	58.3	30.0	13.4	
	TURDIDAE	350	260	74.3	64.2	10.8	0.4	
	TYRANNIDAE	115	28	24.3	50.0	10.7		
	Total:	3532	2057	58.2	67.1	38.6	5.9	
2	CHAEMAIDAE	1	1	100.0				(1)
	CORVIDAE	76	32	42.1	68.8	46.9	3.1	(3)
	FRINGILLIDAE	1738	1184	68.1	18.3	35.0	53.0	
	ICTERIDAE	150	85	56.7	4.7	28.2	34.1	
	MIMIDAE	109	28	25.7	17.9		46.4	(10)
	PARIDAE	176	110	62.5	86.4	5.5	1.8	
	PARULIDAE	623	309	49.6	84.8	5.5	1.0	
	TURDIDAE	228	165	72.4	95.2	38.8	4.2	
	VIREONIDAE	74	41	55.4	56.1	39.0		
	Total:	3175	1955	61.6	40.2	28.4	34.9	

TABLE III (continued)

Strata	Family	Total Birds	Total Positive	Percent Positive	% Leucocytozoon	% Haemoproteus	% Plasmodium	Others
3	AEGITHILIDAE	2						
	ARDEIDAE	2						
	BOMBYCILLIDAE	14	8	57.1	75.0			(2)
	CERTHIDAE	4	1	25.00	100.0			
	COLUMBIDAE	99	98	99.0	12.2	79.6	9.2	
	FALCONIDAE	5	1	20.0	100.0			
	FRINGILLIDAE	195	166	85.1	81.3	51.2	0.6	
	HIRUNDINIDAE	72	6	8.3	33.3			(4)
	ICTERIDAE	634	634	100.0	1.3	94.3	10.1	
	PARULIDAE	418	332	79.4	86.4	41.0	2.4	
	PLOCEIDAE	549	509	92.7		1.6	60.7	
	PICIDAE	60	25	41.7	8.0	100.0		
	SCOLOPACIDAE	2						
	STRIGIDAE	28	18	64.3	100.0			
	STURNIDAE	21						
	VIREONIDAE	3	1	33.3	100.0			
	Total:	2108	1799	85.3	26.3	51.7	21.7	
4	ACCIPITRIDAE	17	11	64.7	90.9			(1)
	ARDEIDAE	3						
	CORVIDAE	9	1	11.1		100.0		
	FRINGILLIDAE	67	55	82.1	49.1	67.3	1.8	
	PICIDAE	36	32	88.9	21.9	87.5	62.5	
	STRIGIDAE	1						
	SYLVIIDAE	40						
	THRAUPIDAE	28	16	57.1	12.5	81.3	6.3	
	Total:	201	115	57.2	40.0	68.7	3.5	

TABLE III (continued)

Strata	Family	Total Birds	Total Positive	Percent Positive	% Leucocytozoon	% Haemoproteus	% Plasmodium	Others
5	ARDEIDAE	8						
	ANATIDAE	4461	1849	41.4	32.5	68.1	19.4	
	COLYMBIDAE	3						
	GRUIDAE	2	2	100.0	50.0	100.0		
	ICTERIDAE	18	18	100.0	94.4			(1)
	PARULIDAE	6	4	66.6	25.0		25.0	(2)
	RALLIDAE	8						
	Total:	4506	1873	41.6	35.9	67.3	14.3	
6	ARDEIDAE	1						
	ICTERIDAE	23	23	100.0			91.3	(2)
	Total:	24	23	95.8			91.3	

It is evident (Table III) that Strata 5 and 6 are less well represented than the other four strata in terms of bird families. It is further noted, that the presence of the Anatidae in the marsh environment, makes the area significant in terms of numbers of birds and parasites. Because of the distinguishing factors of Strata 5 and 6, they are omitted from the general discussion involving the bulk of the birds which occur in the woodland environment. Although there are many less birds reported for Strata 6 (Table III) as compared to Strata 5, the figures comprising this study indicates a heavier infection rate for those birds whose nests are elevated in the marsh environment.

There is an apparent higher incidence of blood parasites in the Fringillids, Icterids, Parulids and Turdids. These groups are observed as well to have representatives in most of the strata within the system. The Fringillidae, as mentioned earlier, are further noted for the fact that they are relatively consistent in its incidence of infection throughout all levels or strata.

In order to better evaluate the hypothesis that a stratification does exist among the various birds reported in the strata system, Figure 4a was constructed to compare the incidence of infection within Strata 1 - 4.

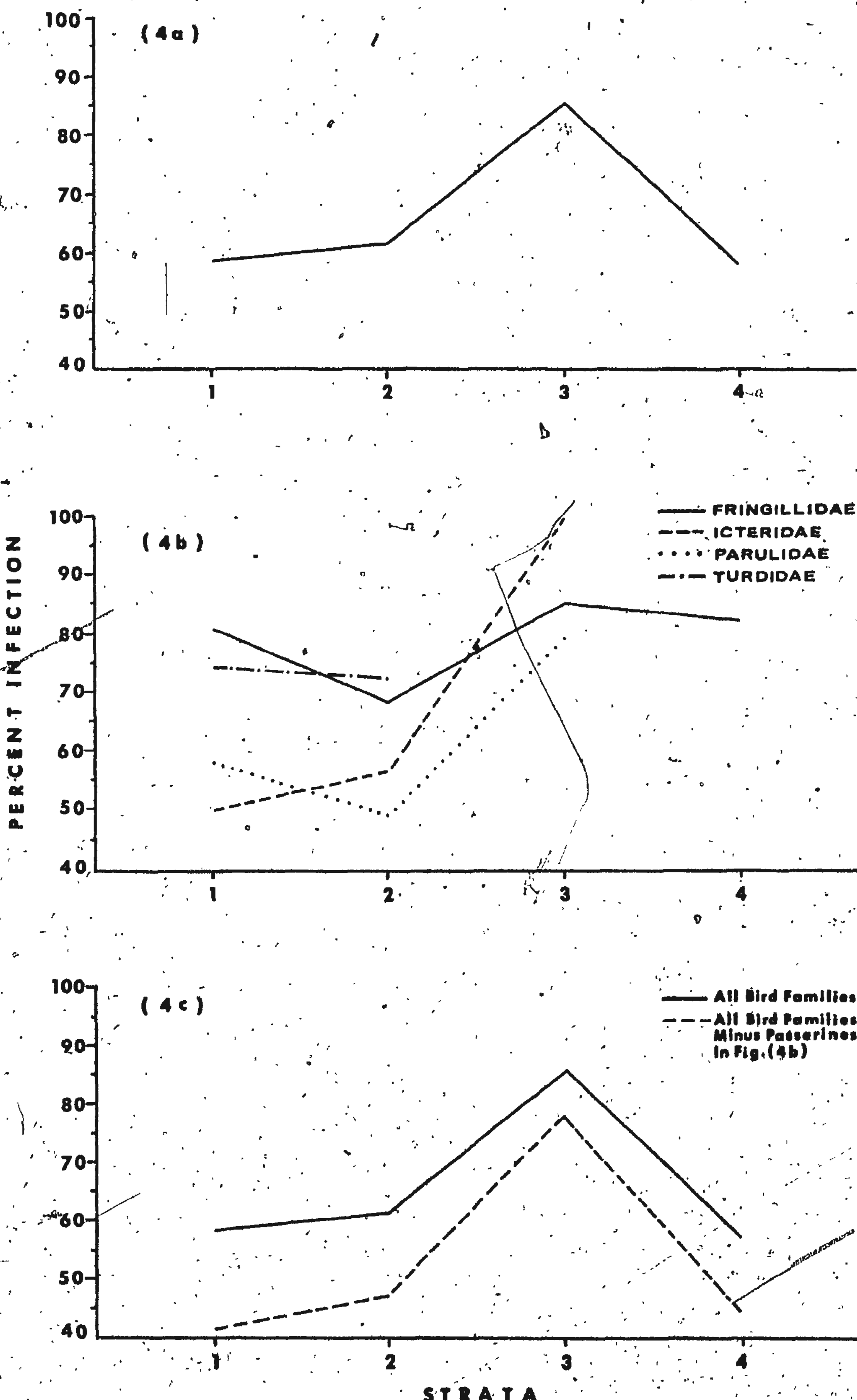
The graph (Figure 4a) shows a definite trend towards a heavier concentration of infected birds in the mid canopy levels and particularly Strata 3. Several statistical tests (Chi-Square

Figure 4.

(a) Overall infection rate for all bird families occupying strata 1, 2, 3 and 4.

(b) Infection rates of four passerine families (Fringillidae, Icteridae, Parulidae and Turdidae) at each of the four strata.

(c) Comparison of all bird families and all families excluding the four passerines in Figure 4b.



(4a)
(4b)
FRINGILLIDAE
ICTERIDAE
PARULIDAE
TURDIDAE
(4c)
All Bird Families
All Bird Families Minus Passerines in Fig.(4b)
PERCENT INFECTION
STRATA

and T-Test) also verified that there was statistical difference between Strata 1 and 3, 2 and 3, 1 and 4, and 3 and 4 at the .05 confidence level. Thus, the expected trend was shown to be statistically significant.

The result of the trend established in Figure 4a and the statistical tests performed on the data also supports similar results obtained previously in Algonquin Park. Bennett and Fallis (1960) suggest that it is more than a mere coincidence that birds with the highest incidence of *Leucocytozoon* usually nest at heights five or more feet above the ground, where many woodland species of ornithophilic simuliids are known to feed. Subsequently, many of the birds with low incidence nest on or near the ground. Bennett (1960) further supports his previous view by noting that his tabular results clearly point out that most of the woodland species of ornithophilic Diptera feed on birds several feet above the ground level.

As the data utilized in constructing Figure 4a is fairly heavily weighted with birds of the four Passerine families (Table II) it was felt that additional analysis (Figure 4b) would be useful in studying the adherence of these birds to the overall pattern. It is observed (Figure 4b) that with the exception of the Turdidae, which were not represented in Strata 3 and 4, the other three groups demonstrate a definite trend towards maximum infection in the mid canopy level of the system.

The downward trend in the Turdidae, from Strata 1 to Strata 2, may have been influenced by the fact that the only species of that family in this study which was designated a habitat other than Strata 1 was *Turdus migratorius*.

To further test the hypothesis that the majority of the birds become infected in the mid canopy levels, it was demonstrated (Figure 4c) that when the Icteridae, Parulidae, Fringillidae and Turdidae are removed from the total birds comprising the present study, a close correlation still exists with the initial trend established in Figure 4a. This information is supported by Bennett (1960) in which he noted that the prime vectors for the transmission of *Leucocytozoon* and *Haemoproteus* are also prominent at this level. In his study, he observed that the ornithophilic flies could be classified into one of two habitats, namely the lakeshore and mid levels of the forest. The latter habitat is known to harbour the specific vectors for the two hematozoon groups mentioned above.

PART II

(NEWFOUNDLAND STUDY)

INTRODUCTION

Prior to the present study, the feeding habits of the adult Simuliidae in Newfoundland were virtually unknown. Previously the only major study area in which work was conducted on the ornithophilic Diptera in North America was in Algonquin Park by Bennett and Fallis (1960), Bennett (1960) and Gollini (1970).

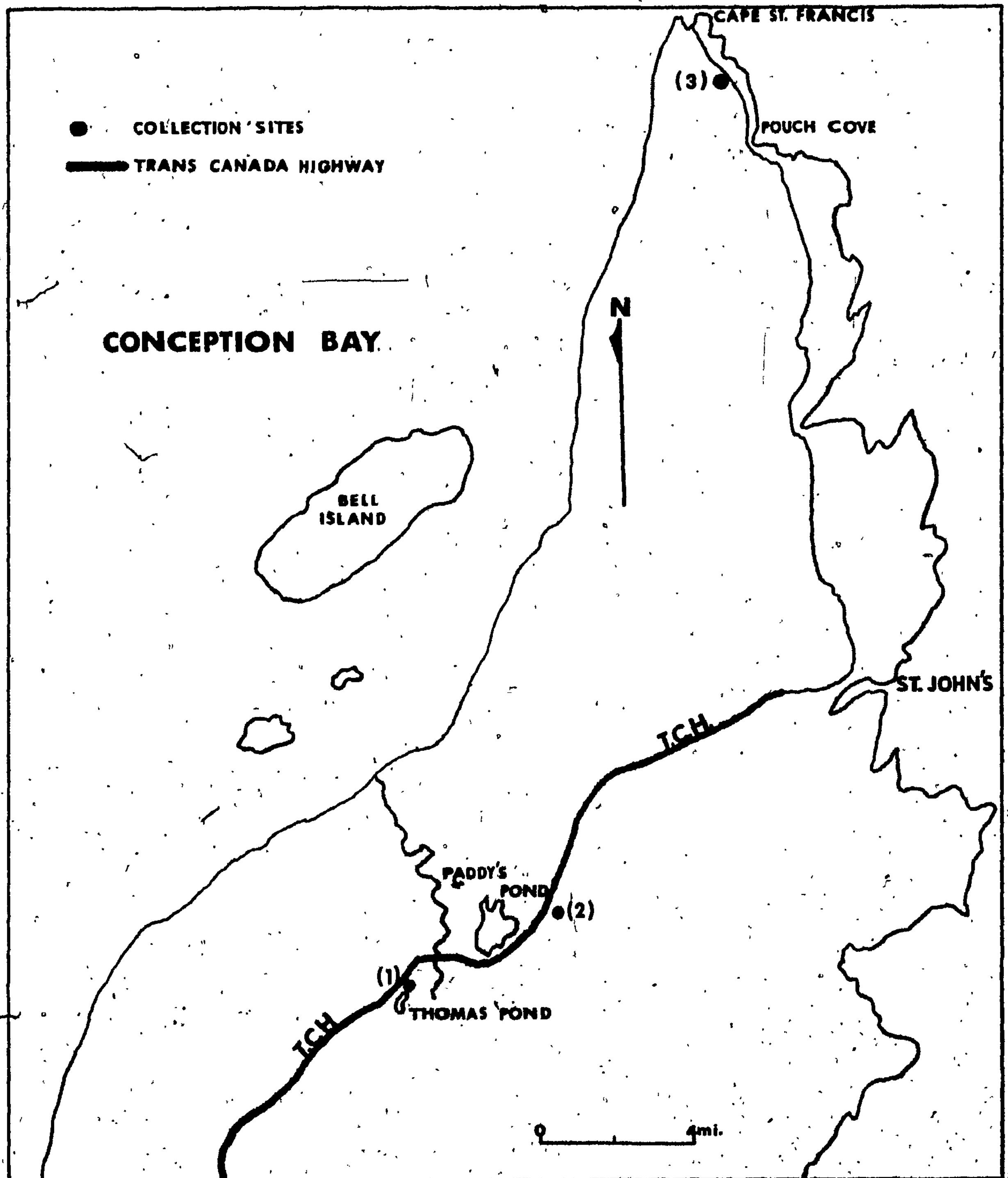
Since 1970 there has been considerable research conducted on the Simuliidae in Newfoundland. Pickavance *et al.* (1970) conducted a study in which some of the Newfoundland species of mosquitoes and blackflies have been identified. Lewis and Bennett (1973) present an extensive record on the simuliid larvae and pupae population of the Island. The results of a four-year survey of the blood parasites of the passeriform birds of the Avalon Peninsula of Newfoundland has only recently been completed (Bennett *et al.* in press).

The present program of research was designed to establish whether the prevalence and distribution of the parasites, hosts and vectors support conclusions of the studies of infections in North American birds. Thus the feeding behavior of the ornithophilic Diptera are studied with a view to obtaining data on the vector potential as it relates to the various groups of avian hematozoa known for the Newfoundland bird population.

An extension of the main function of the thesis was to compare the local Newfoundland results with the data presented earlier in the North American section. It is assumed that certain of the patterns established in North America as a whole, e.g. stratification, host preference, habitat selection, should have an application to the island of Newfoundland.

Figure 5.

Map of Northeast Avalon Peninsula
showing location of the three testing sites:
(1) Manuel's River
(2) Pickavance Creek
(3) Cape St. Francis


CAPE ST. FRANCIS
(3)
COLLECTION SITES
TRANS CANADA HIGHWAY
POUCH COVE
CONCEPTION BAY
N
BELL ISLAND
ST. JOHN'S
T.C.H.
PADDY'S POND
(2)
(1)
THOMAS POND
T.C.H.
0
4mi.

MATERIALS AND METHODS

The field work for this study was conducted during the summers of 1970, 1971 and 1972 in three general areas (Figure 5) on the Avalon Peninsula region of Newfoundland within an approximate radius of 16-32 km. from the Memorial University Campus in St. John's.

A. DESCRIPTION OF TESTING AREAS

I. Pickavance Creek

The major portion of the research was conducted in the Pickavance Creek area (Pickavance *et al.*, 1970; Lewis and Bennett, 1973; Bradbury and Bennett, 1974;) which is located approximately 16 km. west of St. John's on the margins of the Trans Canada Highway. This stream and its environs has been extensively described by Lewis (1973); Lewis and Bennett (1973); Bradbury (1972); and Bradbury and Bennett (1974).

The stream flows through the forest in the area which provides an excellent sheltered location for collecting ornithophilic flies. Several sites were tested (utilizing bait birds and sweep nets) along the stream prior to the selection of a "permanent" testing site on the basis of 1. abundance of ornithophilic simuliids 2. accessibility 3. shelter from wind.

A second testing site within the Pickavance Area referred to as the "Knoll" was tested on a number of occasions to compare these results with the "permanent site" which was located approximately 100 m. away. The major physical differences between the two was that the "permanent site" was within 2 m. of the stream and was slightly below the level of the highway whereas the "knoll" was at a much higher elevation (20 m.) above the road and a considerable distance from the stream.

II. Manuel's River

Manuel's River lies approximately 4.8 km. west of the Pickavance on the Trans Canada Highway and has similar vegetation to the latter area. The damming and enlargement of Thomas Pond has left the testing site, utilized in the Manuel's River area, as nothing more than an overflow from the pond, which, during the study was frequently reduced to a mere trickle. The overall area was less heavily forested than the Pickavance area, had fewer streams and was markedly influenced by winds blowing off Thomas Pond.

III. Cape St. Francis

Cape St. Francis was the third major area tested in this study and in contrast to the other two was significantly different in practically all of its aspects. The area is located approximately 32 km. north of the university campus, overlooking the North Atlantic Ocean. It has been described (Bennett *et al.* 1974) as a "Marine" barrens situated on high rocky bluffs with extensive glacial tills at the base. The vegetation of the region consists mainly of short, dense, wind-deformed conifers in sheltered hollows, and a ground cover of grasses and heaths interspersed with many exposed areas. The climatic conditions can be generalized as one in which it is directly influenced by high winds and frequent foggy periods. The streams and marshes in the region are minimal.

Utilization and physical characteristics of the four areas are summarized in Table IV.

TABLE IV

Comparison of Testing and Physical Features of three Newfoundland Test Areas.

	PICKAVANCE CREEK		MANUEL'S RIVER	CAPE ST. FRANCIS
	Permanent Site	Knoll		
Frequency of Streams	Permanent Stream in Area	100 m. from Stream	Stream fluctuated, often a mere trickle	Minimal
Frequency of Wind	Generally unaffected	Generally moderate	Generally moderate-high	Generally high
Frequency of Fog*	3/27	1/8	4/12	8/10
Average Temperature**	22°C.	21°C.	21°C.	18°C.
Total No. Days Tested	27	8	12	10
Test Method	Pre-selected Tree Hoist	Portable Hoist	Portable Hoist	Portable Hoist
No. Flies collected from Bait Birds	350	89	108	54
Mean Flies/Bird Hour	3.2	2.8	2.3	1.4
Collecting Times	1800-2200 hours	1800-2200 hours	1800-2200 hours	1800-2200 hours

* No. of test days fog encountered, compared with total test days.
** Average temperature for collecting days during 3 year study period.

B. COLLECTION TECHNIQUES

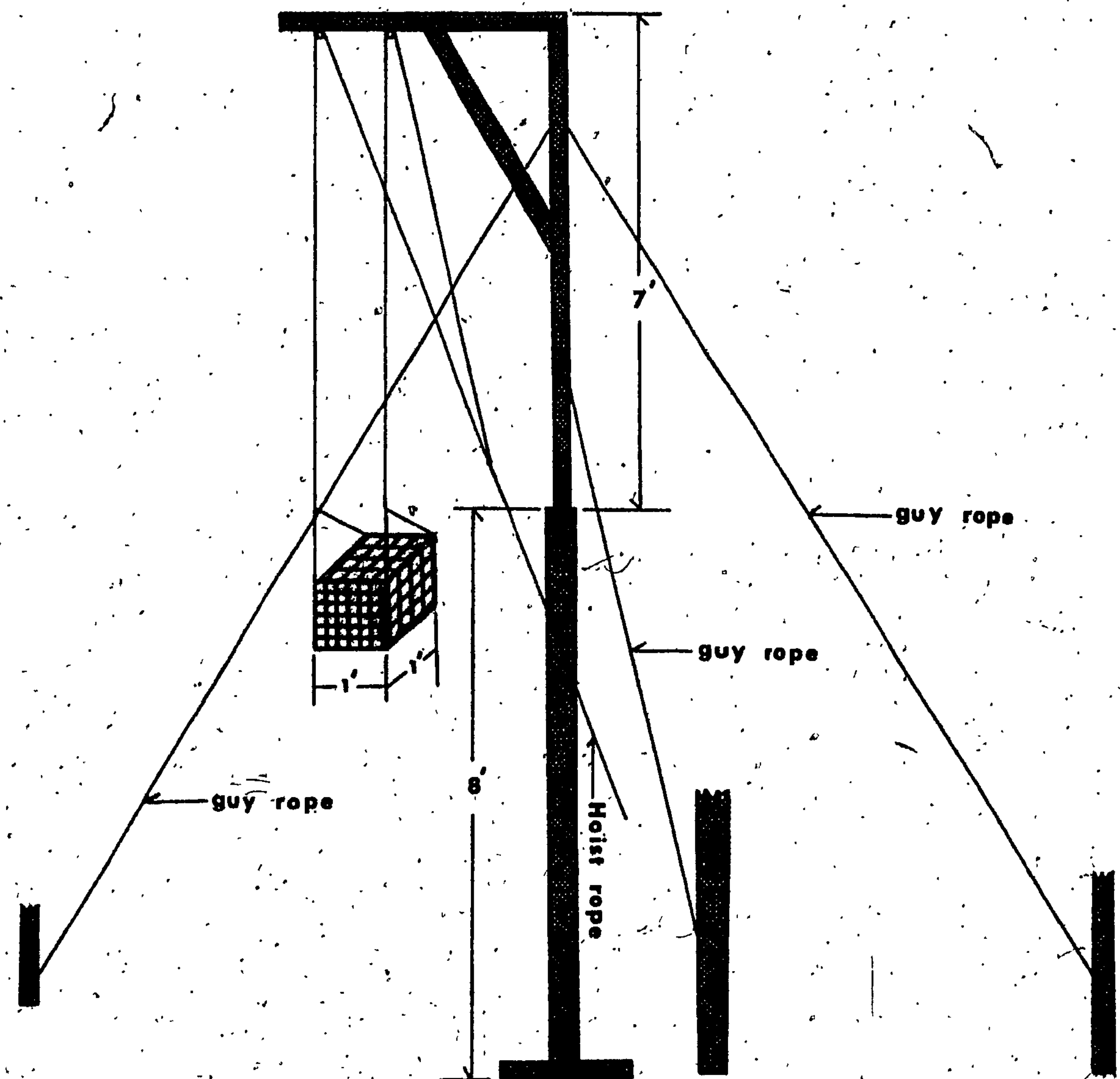
I. General

At the initiation of the study, the techniques described by Bennett (1960) for the collection of ornithophilic biting flies, were applied to the present investigation. Minor modifications during the first season, however, were necessary to accommodate the local conditions. The modifications were: 1. Almost total elimination of ground testing, which yielded statistically insignificant numbers of fed flies 2. Restriction of collections to the forest and stream habitat as opposed to the lakeshore habitat which was tested in Bennett's study 3. Bantam hens were the main bait birds utilized by the author whereas Bennett made use of diverse bird species which were kept in captivity. (In the present study this procedure was not used because of lack of facilities). 4. The height above ground utilized for collections of fed flies was somewhat lower than that in Algonquin Park.

In each of the test areas an attempt was made to select a site based on the shelter provided and the location of a suitable tree for the elevation of the birds to the appropriate level for the attraction of the ornithophilic flies. The only case in which a suitable tree could be selected for consistent testing was the Pickavance "permanent" site. The other areas required the use of a portable hoist (Figure 6) which was constructed for this purpose.

Figure 6.

Portable Hoist, utilized for elevation of bait birds in test areas. (Scale illustrates the dimensions of the apparatus)


7'
guy rope
guy rope
1'
1'
8'
Hoist rope
guy rope

II. Simuliids and Ceratopogonids

Bantam hens which had proved to be successful bait birds elsewhere (Bennett 1960; Smith 1966) were used successfully for the attraction of the ornithophilic simuliids and ceratopogonids. At different intervals during the study period ducks were also introduced as bait birds.

Collections of ornithophilic hematophagous flies were essentially as described by Bennett (1960). The birds were held in wooden framework cages of 12 inches cube, covered by heavy 1 inch mesh. The heads of the birds were covered by chamois hoods, which kept the birds relatively motionless and prevented the feeding flies from being dislodged or devoured. As a number of birds were kept on hand (primarily females because they are more docile), birds were seldom used on two successive days to avoid excessive stress on any one.

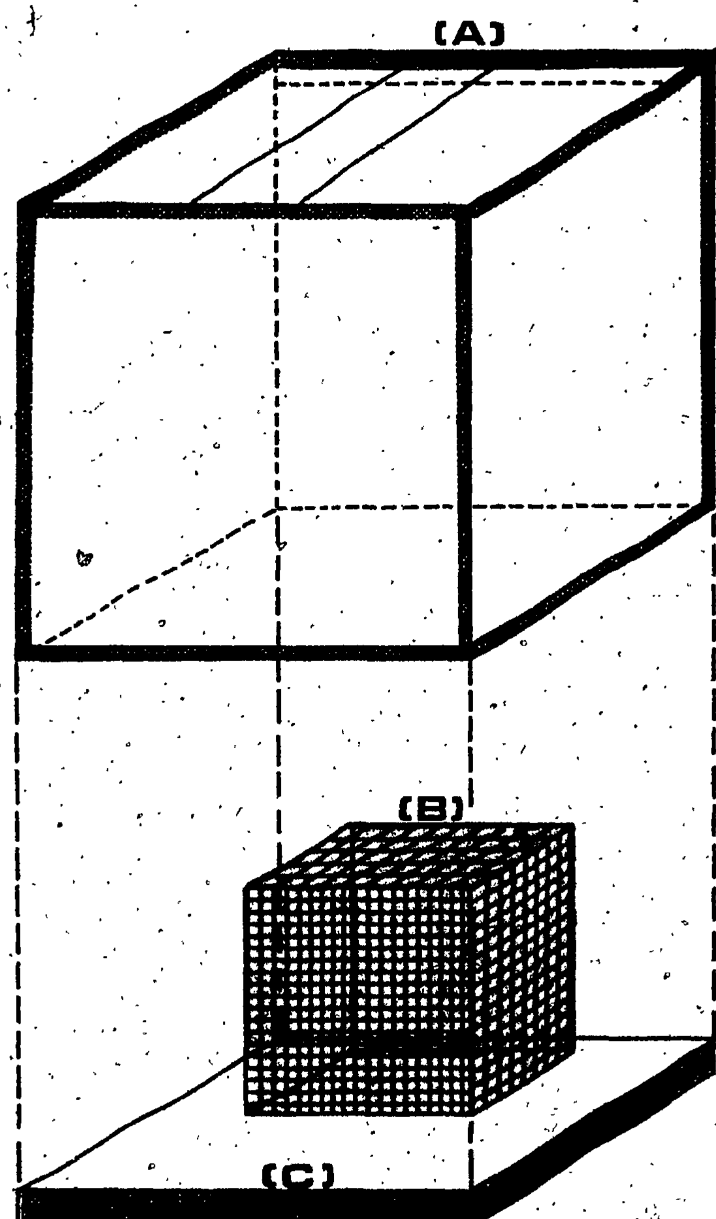
During ground collections the exposure cages containing the birds were placed on 2 foot squares of plywood at the test sites. The birds were exposed for 20 - 30 minutes, following which they were covered by a collecting cage. The collecting cage consisted of a wooden framework of 2 feet cube, covered with nylon screen (60 meshes to the inch) on five sides, leaving the bottom open. Weather stripping, glued to the bottom frame of the cage, formed a tight seal with the plywood base and prevented escape of the flies. The birds were left under these collecting cages for 20 - 30 minutes after which time the engorged flies were collected. Flies were collected, using aspirators, through a sleeve at the top of the cage (Figure 7).

Slight modifications of the procedure were required when collecting flies from different heights. The birds, in the exposure cages, were raised to the desired height (generally 15 feet) by a simple rope and pulley system, previously secured to the tree. A four point attachment of two ropes to the exposure cage prevented it from spinning in the air. The cages were raised to the desired height in approximately ten seconds and left there for 20 - 30 minutes. Following this they were lowered carefully to the plywood squares and the engorged flies collected as previously described.

A portable hoist (Figure 6) was constructed for use in areas where desirable trees could not be found for the attachment of the pulley system. The hoist was constructed of two pieces of light-weight wood measuring 2 inches square and 7 feet long. These two lengths fitted together to give a combined height of approximately 15 feet. A cross bar of the same material approximately 3 feet in length was used for the attachment of the pulley system. Three guide ropes attached to the vertical sections and tied to the small trees or shrubs provided a stable apparatus to support the birds in their cages at heights up to 14 - 15 feet. The same procedures for raising and lowering the birds applied as discussed earlier.

Figure 7.

Illustration of collecting and exposure (holding) cages utilized in the collection of ornithophilic Diptera. Collecting cage (A) has opening at top which provides access for removal of engorged flies. Exposure cage (B) is positioned on plywood board (C).



(A)
(B)
(C)

Following removal of the engorged flies from the collecting cages or subsequently the aspiration of mosquitoes from the author's body, the flies were stored in modified CDC cardboard containers (Collins *et al.*, 1962) and conveyed to the temperature control chamber at the university, where they were held at 16°C. and high humidity.

The covers of the containers had fine nylon mesh tops which provided a means for supplying the flies with water which was accomplished by placing a piece of saturated tissue paper on the surface. A trap door consisting of dental rubber dam provided access to the flies for future examination. Inside each container a sugar cube was placed to provide nourishment for the engorged flies.

III. Mosquitoes and Hippoboscids

Mosquitoes were collected primarily by netting them about the author or by aspirating them directly from the author's skin as they engorged. So few mosquitoes were taken from the bait birds that this method was the only successful one for obtaining these Diptera, as the use of other trapping forms are not practical in Newfoundland because of vandalism.

Hippoboscids were taken entirely from native birds trapped in mist nets by Bennett during the same time and location as this study. At no time were these flies observed on or near the bait birds, as might be expected (Bequaert, 1953).

C. EXAMINATION OF ENGORGED FLIES

In the laboratory the flies were identified and then dissected with a view to examining the salivary glands and hindgut for sporozoites and trypanosomes (Bennett, 1960).

Following removal from the holding containers, the flies were chloroformed and then dissected on a clean microscope slide. A second slide containing two separate drops of saline were the receptacles for the hindgut and the salivary gland. A cover slip was placed on the slide and then both structures were examined for the presence of parasites. This method was employed for the four groups of flies under study.

D. WEATHER AND CLIMATIC CONDITIONS

For the duration of the field work a log was maintained on the general weather conditions experienced in the research area. During any given day in which flies were collected, notes were made on air temperature, cloud cover, wind conditions and time of sunset. In addition to these reports, information obtained from the Meteorological Office, St. John's Airport enabled the presentation of weather synopsis for the three collecting seasons.

In 1970 the mean monthly air temperature for late June to mid July ranged from 14° - 22°C., with an occasional night going below 12°C. During the latter part of July and all of August the temperatures were generally higher ranging from 22° - 30°C. Precipitation was extremely low and there was usually a slight breeze of wind blowing in the research area. The high temperatures and dry conditions reduced Pickavance Creek to a mere trickle which was reflected in the low numbers of flies collected.

In 1971, relatively high temperatures were still experienced but the general climatic conditions (precipitation and wind) were not as drastic as the previous year. It proved to be a much better season for collecting purposes.

The final year (1972) was very similar to 1970 and once again the number of flies collected were much reduced.

RESULTS AND DISCUSSION

FIELD AND LABORATORY OBSERVATIONS

Preliminary observations, conducted in the field, suggested that certain groups of hematophagous Diptera were relatively abundant whereas others were absent or generally unattracted to the bait birds. The latter observation was particularly true in the occurrence of the mosquitoes and hippoboscids. The former group amounted to a single blood fed specimen, which also represents the total number attracted to the birds during the study. Hippoboscidae were even more elusive in that they were at no time observed by the author in the field.

Bennett, Campbell and Cameron (1974) in a survey of 2675 passeriforms in Newfoundland, found 80% to harbour blood parasites. The breakdown of these parasites was 92% of the infected birds harboured *Leucocytozoon*, 22% *Haemoproteus*, 17% *Trypanosoma* and 2% *Plasmodium*. From these figures it was assumed that the vectors of *Leucocytozoon* and *Trypanosoma* (ornithophilic simuliids) would be the most numerous, followed by Ceratopogonidae as vectors of *Haemoproteus* and mosquitoes as the transmitting agents of *Plasmodium*.

Species of Simuluiidae and Ceratopogonidae

Following several trips to the research areas it became apparent and later verified (Table V) that the most abundant

TABLE V

Total ornithophilic flies and total infected flies collected in three Newfoundland test areas: (1) Manuel's River (2) Pickavance Creek (3) Cape St. Francis (see Figure 5) during 1970, 1971 and 1972.

	Total Examined	Total Positive	Percent Positive
SIMULIIDAE			
S. latipes	390	110	28.2
S. aureum	24	6	25.0
S. gouldingi	3		
Total:	417	116	27.8
CERATOPOGONIDAE			
C. stilobezzoides	184	25	13.6
Total:	184	25	13.6
MOSQUITOES	197	15	7.6
Total:	197	15	7.6
HIPPOPOSCIDAE	101		
Total:	101		
OVERALL TOTAL:	899	156	17.4

ornithophilic flies were the simuliids. In several instances mammalophilic species, particularly *S. venustum* were removed from the collecting cages, but at no time were they observed to have fed on the birds. The only forms which had taken a blood meal were the ornithophilic flies which were recognized by the presence of a bifid tarsal claw (Shewell, 1955).

Unlike the situation reported in Algonquin Park by Bennett (1960) who showed 9 - 10 species of ornithophilic Simuliidae, only 3 species, viz.

Simulium (Eusimulium) latipes auct. nec Meigen

Simulium (Eusimulium) aureum Fries

Simulium (Eusimulium) gouldingi Stone

occurred in the Avalon study area. Of these, the majority collected were the *latipes* type (Table V). Lewis (1973) concludes that this species comprises the major percentage of the total ornithophilic blackfly population in small streams.

In his study Lewis recorded 21 species of simuliids from insular Newfoundland, of which 11 are thought to be ornithophilic. However, only two of the eleven bird feeders are abundant; *S. latipes* is widespread throughout the island, while *P. pleurale* is apparently abundant only in Western Newfoundland. In the present study *S. latipes* was also found to be heavily infected with *Leucocytozoon* and appears to be the prime vector for this genus of parasite in the avian population.

S. aureum was collected in much smaller numbers than *S. latipes* but the infection rate was generally similar (Table V). *Simulium gouldingi* was only collected on two occasions and like *aureum* was restricted to the Manuel's River area. Its small numbers and absence of sporozoites and trypanosomes has resulted in its exclusion from the statistical portion of this study. Lewis (1973) reported it as a new record for the area and notes that it was restricted to six streams all on the Avalon Peninsula.

The only other major group of hematophagous Diptera which were collected in the "fed" condition were the Ceratopogonidae. The midges collected in this survey were restricted to one species, namely, *Culicoides stilobezzioides*. The species was generally represented by a large number of individuals and as it has been proven to be a vector for *Haemoproteus (Parahaemoproteus) canachites* and *H. velans*, etc. by Fallis, Bennett, Khan, etc., it is assumed to be the only vector in this area. It is illustrated (Table V) that only 44.1% as many midges were collected as compared to the blackflies, and it is further observed that the infection rate is much lower than in the simuliids (13.6% as compared to 27.8%).

Species of Mosquitoes and Hippoboscids

Several species comprise the mosquito collection in the present study. However, as these flies were not removed from the bait birds, but rather collected using a sweep net, the results (Table V) represent the mosquitoes as a whole and does not include a species breakdown. The majority were *Aedes* (*Ochleratatus*) *punctor* Kirby. Pickavance *et al.* (1970) established that this mosquito was the most abundant species on the Avalon.

Ornithomyia fringillina was the only hippoboscid examined in this survey. All flies were taken from birds with *Haemoproteus* (*Parahaemoproteus*) *fallisi*, *H. fringillae* or *H. orizivora*. As no infected hippoboscids were found, these results agree with Bennett and Fallis (1960); Fallis and Bennett (1961); findings and indicate they are not vectors in the Newfoundland region.

Following collections of the fed flies, the insects were examined in the laboratory for the presence or absence of blood parasites. The actual breakdown of these infections (Table VI) as observed in the hindgut and salivary glands are noted for the various ornithophilic flies reported in Table V.

It is observed that the simuliids, ceratopogonids and mosquitoes harboured parasites of hemosporidia. The sporozoites recorded for the salivary glands were either members of *Haemoproteus*, *Leucocytozoon* or *Plasmodium* depending upon the particular vector involved. It is immediately apparent that the Simuliidae (vectors

TABLE VI

Hindgut and salivary gland infections of the four groups of ornithophilic flies collected in the three Newfoundland test areas.

	Overall Prevalence	Infected Flies Hindgut* Percent	Infected Flies Salivary Glands** Percent
SIMULIIDAE	27.8%	75.0	52.2
CERATOPOGONIDAE	13.5%	75.0	16.6
MOSQUITOES	7.6	100.0	7.1
HIPPOPOSCIDAE	0.0%	0.0	0.0

*Trypanosomes, assumed to be *T. avium*

**Sporozoites of *Leucocytozoon*, *Haemoproteus* and *Plasmodium*.

of *Leucocytozoon*) had the highest sporozoite rate, which was approximately three and a half times higher than the next closest group Ceratopogonidae (vectors of *Haemoproteus*). This agrees with the findings of Bennett *et al.* (1974) in their study of Newfoundland passeriform birds.

It is assumed from the results of Bennett *et al.* (1974) that the sporozoites of *Leucocytozoon* represented in order of their frequencies of occurrence belong to: *L. fringillinarum*, *L. dubreuili* (comprising the bulk of the species) and *L. majoris* and *L. sahkaroffi* constituting the minor percentage of the total blood parasites.

Similarly, the sporozoites of *Haemoproteus* were believed to be those of *H. orizivora/fringillae* or *H. fallisi*. Sporozoites of *Plasmodium*, although only observed in one or two cases in the present study, were either those of *P. vaughani*, *P. circumflexum* or *P. relictum*, probably the former, as this was the most common *Plasmodium* in the passeriform birds of the area.

The low incidence of gland infection in the mosquitoes indicates an absence or apparent low rate of *Plasmodium* transmission in Newfoundland. Bennett *et al.* (1974) points out that this malarial parasite was uncommon and further suggests that the absences may reflect the insularity of Newfoundland. These parasites are relatively abundant in birds from adjacent mainland locations.

The hindguts of many of the biting fly species examined, with the exception of the hippoboscids, harboured trypanosomatids. It is possible that many of these were stages of normal flagellate parasites of insects. However, in view of the reports of Baker (1956) and Bennett (1961), the fact that the flagellates were confined to the hindgut, and the fact that most flagellate infections occurred in flies harbouring sporozoite infections, it was concluded that these flagellates were most likely to be the insect stages of *T. avium*.

OBSERVATIONS ON FEEDING BEHAVIOR OF ORNITHOPHILIC DIPTERA

From the field records maintained over the duration of the study period, information regarding the prime periods and conditions for collections of blood fed flies as well as their abundance was examined and is reported in this section (Table V).

As was the case in Algonquin Park (Bennett, 1960), the best times for collections of the crepuscular ornithophilic flies, was from 1800 to 2200 hours. Ten trials conducted at other times of the day were generally unsuccessful in terms of collecting blood fed flies. On several occasions early morning collections (500 - 800 hours) yielded a small number of *S. latipes*, again agreeing with the pattern in Algonquin Park.

The single, most profitable time for collections was observed to be when the humidity was high, when there was a slight breeze and the temperature was between 19° - 24°C. During these periods the collections of blackflies, in particular, were at a maximum.

Due to the climatic and weather conditions in Newfoundland the biting fly season (ornithophilic and mammalophilic) is retarded when compared with similar regions on the mainland, (Lewis, 1973). It is noted that due to an extended winter the streams probably warm up more slowly in the spring in Newfoundland than they do in other regions. This, would explain the adult emergence occurring a month later in Newfoundland than in Ontario.

The testing period in this study ran from the last two weeks in June to the end of August. During this time it was noted that the peak biting period was from early July to late August for all ornithophilic species. Lewis (1973) also established a similar pattern with respect to the emergence of the adults based on larval and pupal studies.

The low numbers of blood-fed flies taken on any given collecting day (15 - 20) in Newfoundland was in sharp contrast to that reported for Algonquin Park, where several hundreds could be collected on an optimal evening.

Following three summers field work it was evidenced that not only are the species of ornithophilic flies restricted in Newfoundland, but the numbers are far lower compared with reports from mainland areas (Gollini, 1970; Bennett, 1960). Studies conducted by Lewis during the same time as the present one also confirms that a much reduced bird biting fly population exists in Newfoundland.

In Newfoundland, an approximate average of 5 flies/bird hour was collected under optimal conditions, averaging possibly 2.6 fly/bird hour over the season; but in Algonquin Park a figure of 300 - 400 flies/bird hour could be optimally obtained, averaging 15 - 20 flies/bird hour over the season. In addition, only 27.8% of the simuliids harboured sporozoites of *Leucocytozoon* in Newfoundland whereas nearly 80% were vectors in Algonquin Park at the end of the season.

Despite this large difference in both simuliid numbers and vector potential, 82% of the passeriform birds from this study area in Newfoundland harboured *Leucocytozoon*, (Bennett, pers. comm.) while Bennett and Fallis (1960) reported a *Leucocytozoon* prevalence of approximately 70% in Algonquin Park. The similarity of the two prevalence rates is striking, and is significant as it shows that a low vector potential (as measured in flies/bird hour) using similar trapping techniques can produce a prevalence of hematozoa in the passeriform population equivalent to that produced by a vector potential of 60 - 100 times greater. This fact clearly indicates that vector numbers, per se., are not the major factor contributing to high transmission in the avifauna. Rather, it suggests the presence of a highly developed host-parasite-vector relationship of exceptional efficiency.

Habitat Preference

In an attempt to ascertain whether a habitat preference for the vectors existed in Newfoundland, testing during the first season was carried out in a number of areas and at different levels in the woodland habitat. Prior studies, (Bennett, 1960; Gollini, 1970) suggests that some species of flies were more abundant in some habitats than in others. These studies were conducted in Algonquin Park where some of the physical and biological factors differ significantly from the Newfoundland situation. For instance, the forest habitat generally has a much higher canopy and the numbers and species of ornithophilic flies were considerably greater than those reported in the present study.

Testing in the mainland area was performed in two general habitats, i.e. the lakeshore and the woodland (forest) habitat. In the current study, testing was confined primarily to the woodland environment and involved only the sylvatic flies. The lack of testing of the lakeshore habitat in this study was compensated for, in that a stream (Pickavance Creek) flowed very close to the actual collecting site. In both cases there was a concurrence of the ideas that typical lakeshore species were absent from the sylvatic habitats and typical canopy simuliids were not found in significant numbers at the lakeshore or at ground level in the forest.

It is the finding of this study that the ornithophilic flies (simuliids and ceratopogonids) were restricted primarily to the 10' - 20' level or strata in the woodland habitat. This in effect is the mid and top canopies in the Newfoundland environment (Figure 1). Ground level testing provided such small numbers, that following the first season, collections were concentrated mainly at the 15 foot level. It was found to be the most successful strata for obtaining reasonably large samples of blood fed blackflies and midges. This information is supported by the studies of Bennett (1960) and Gollini (1970) in which they showed that the preferred habitat for the woodland ornithophilic simuliids (*S. latipes*) as well as *Culicoides stilobezzoides* is the canopy level.

Gollini's collection (Algonquin Park) of 6980 Simuliidae from the canopy habitat shows that of the ornithophilic forms, the great majority consisted of *S. latipes* and *S. aureum*. Similarly, from a total of 5,029 collected from the ground, less than one percent consisted of the two ornithophilic forms. Ninety-nine percent consisted of the mammalophilic species, namely *S. venustum*. Bennett (1960) utilizing simultaneous exposures of crows at four heights above the ground in the forest habitat (0,5,10,20 ft.) shows that *Simulium aureum*, *S. latipes* and *Culicoides stilobezzoides* were heavily concentrated in the five and ten foot levels with considerably lesser numbers on the ground and high canopy. This supports the view that most woodland species feed on birds several feet above the ground, but he is very explicit in pointing out that there is no evidence of a preferred stratum between 5 and 20 feet. Gollini (1970), however, suggests that the habitat preferences of the simuliids are far more rigid than that indicated by Bennett.

In the present study, where the height of the canopy is considerably reduced, it is very difficult to determine whether or not there is a preference between the mid and high canopies. It can, however, be concluded, that there is a preference to the 10 - 15 foot level as opposed to the ground habitat. This stratification or preference was very clearly demonstrated over the three year period and agrees with the results of the North American section of the present study (Figure 4a).

NEWFOUNDLAND BIRD SURVEY

The clearly indicated strata preference of ornithophilic simuliids demonstrated by Bennett and Gollini and confirmed in this study for Newfoundland, was assumed to play a major role in the host-parasite-vector relationship. If this assumption is true, then birds which normally nest in or inhabit specific strata should demonstrate a prevalence of blood parasites appropriate to the vector potential of that strata, even though few flies may be involved.

In order to test the premise stated above, a total of 1314 birds of seven species were examined (Table VII). The birds studied were all passeriforms and consisted of the following species: swamp sparrow, fox sparrow, Wilson's warbler, robin, northern water thrush, olive backed thrush and eastern black-poll warbler.

The reasons for the selection of these particular species were: (1) they had been previously stratified in the North American results section (2) they are represented in large enough numbers to constitute a reasonable sample size (3) these birds are common Passerines of Newfoundland (4) they were collected from the three locations utilized in the present study.

From the data (Table VII) it is evident that the stratification is not as clearly defined for the seven selected Newfoundland bird species, as that exhibited in the overall North

TABLE VII

Parasite prevalence of 1314 Newfoundland passeriform birds utilizing the strata system. Included is a breakdown of the three Newfoundland test areas.

Strata	Bird Family / Species / Test Area	Total	Total Positive	Percent Positive	% Leuco-cytozoon	% Haemo-proteus	% Plas-modium
	FRINGILLIDAE						
1.	*Passerella iliaca*						
	Cape St. Francis	50	29	58.0	96.5	34.5	
	Pickavance Creek	132	126	95.5	89.7	50.0	
	Manuel's River	154	143	92.9	93.0	48.3	
	Total:	336	298	88.7	91.9	47.7	
2.	*Melospiza georgiana*						
	Cape St. Francis	6	5	83.3	100.0		
	Pickavance Creek	46	44	95.7	100.0	50.0	
	Manuel's River	43	41	95.3	87.8	60.9	
	Total:	95	90	94.7	94.0	52.2	
	PARULIDAE						
1.	*Seiurus novaboracensis*						
	Cape St. Francis	16	11	68.8	90.9	9.1	
	Pickavance Creek	146	124	84.9	98.4	59.7	2.4
	Manuel's River	112	93	83.0	92.5	15.1	2.2
	Total:	274	228	83.2	95.6	39.0	2.2

TABLE VII (continued)

Strata	Bird Family Species Test Area	Total	Total Positive	Percent Positive	% Leucocytozoon	% Haemoproteus	% Plasmodium
	PARULIDAE						
2.	*Wilsonia pusilla*						
	Cape St. Francis	8	7	87.5	100.0		
	Pickavance Creek	76	56	73.7	98.2	2.0	
	Manuel's River	49	37	75.5	99.0	3.0	
	Total:	133	100	75.2	98.0	2.0	
3.	**Dendroica striata*	260	222	85.4	92.8	41.4	4.0
	Total:	260	222	85.4	92.8	41.4	4.0
	TURDIDAE						
1.	*Catharus ustulatus*						
	Cape St. Francis	3	2	66.6	50.0		
	Pickavance Creek	34	32	94.1	90.6	90.6	
	Manuel's River	31	21	67.7	100.0	19.0	
	Total:	68	55	80.9	92.7	60.0	

*Specific locations unknown for this species

TABLE VII (continued)

Strata	Bird Family Species Test Area	Total	Total Positive	Percent Positive	% Leuco-cytozoon	% Haemo-proteus	% Plas-modium
	TURDIDAE						
2.	*Turdus migratorius*						
	Cape St. Francis	11	8	72.7	75.0	62.5	
	Pickavance Creek	101	99	98.0	99.0	54.5	
	Manuel's River	36	34	94.4	100.0	50.0	
	Total:	148	141	95.3	97.8	53.9	

American trend (Figure 4a). As the overall infection rate in Newfoundland (80%), as determined by Bennett *et al.* (1974) is much higher than that obtained in Algonquin Park, it might be expected that the birds at all "levels" in Newfoundland would have a higher parasite prevalence. This is shown to be the case (Table VII) and has the general effect of reducing the marked difference between the four strata as displayed in the North American results of the present study.

An additional factor, which makes the stratification of Newfoundland birds a more difficult task when related to other surveys is the absence of a high canopy. In effect it can be stated, based on the present study, that the strata 4 level, is non existent in Newfoundland. This further suggests that birds which normally nest in this habitat would be either less abundant or when present would select nesting sites at a lower level in the woodland environment.

Although the Newfoundland avian situation is shown to have special characteristics, there is still a case for establishing a stratification to determine at which level in the woodland habitat, maximum infection occurs. Allowing for the exception of *Seiurus novaboracensis* and *Wilsonia pusilla*, it is observed (Table VII) that there is a higher infection rate at the higher strata than at ground level. This agrees with the findings of Bennett and Gollini in Algonquin Park.

To further illustrate the application of the stratification established earlier (Figure 4a) a greater number of Parulid species were examined (Table VIII). It is noted that this group was shown in the North American section to demonstrate a definite habitat preference which was correlated with parasite prevalence. Although there were lesser numbers of individuals occupying strata 2 and 3 (Table VIII), there is still an apparent higher parasite prevalence at these two levels.

The specific parasite prevalence, as determined by the *Leucocytozoon*, *Haemoproteus* and *Plasmodium* infections is presented in Figure 8. As these results were abstracted from Table VII it represents the situation in a relatively large sampling of common Newfoundland Passeriforms.

The bar diagram illustrates the *Leucocytozoon* infection in the Newfoundland avifauna and agrees with the higher rate of sporozoites in the simuliids (Table VI) as well as the results of Bennett *et al.* (1974). The *Haemoproteus* infection is noted to be less than half that of the birds infected with *Leucocytozoon* and again agrees with the Ceratopogonidae data (Table VI). As noted earlier, the *Plasmodium* prevalence is low and clearly indicates that the parasite is uncommon in Newfoundland birds.

TABLE VIII

Parasite prevalence of Newfoundland Parulidae, utilizing the strata system.

Strata	Bird Species	Total Birds	Total Positive	Percent Positive
2.	*Dendroica petechia*	2	2	
	Mniotilta varia	39	24	
	Oporornis philadelphia	15	13	
	Wilsonia pusilla	133	100	
	Setophaga ruticilla	20	8	
	Vermivora peregrina	25	10	
	Vermivora ruficapilla	5	5	
	Total:	239	152	63.6
3.	*Dendroica palmarum*	81	50	
	Dendroica pinus	26	21	
	Dendroica striata	230	200	
	Total:	337	271	81.3

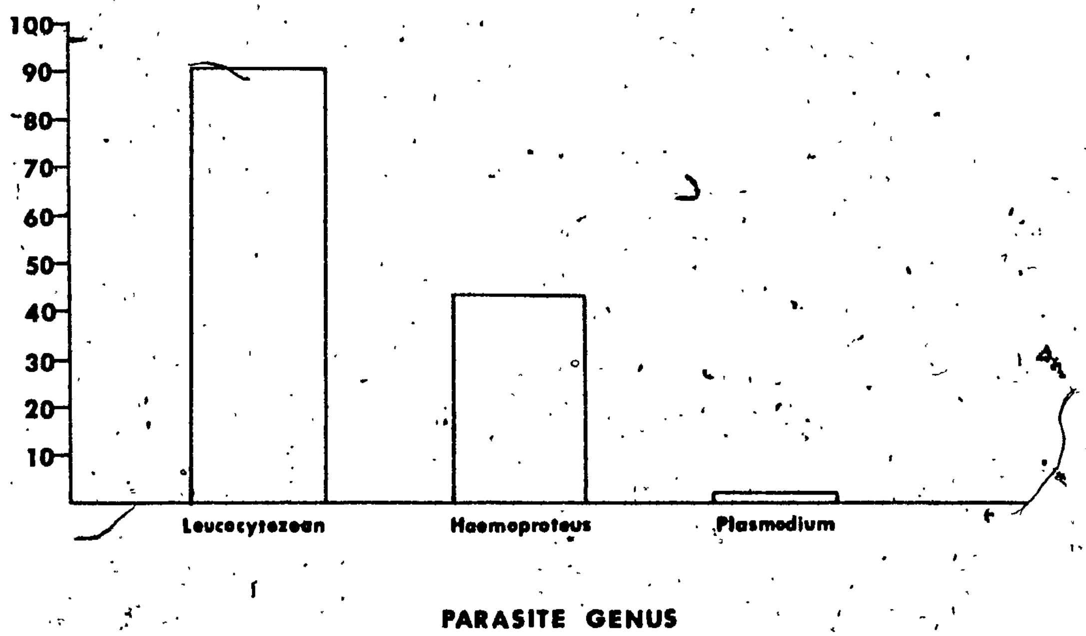
Figure 8.

A comparison of the incidence of *Leucocytozoon*, *Haemoproteus* and *Plasmodium* in 1314 Newfoundland passeriform birds.

Figure 9.

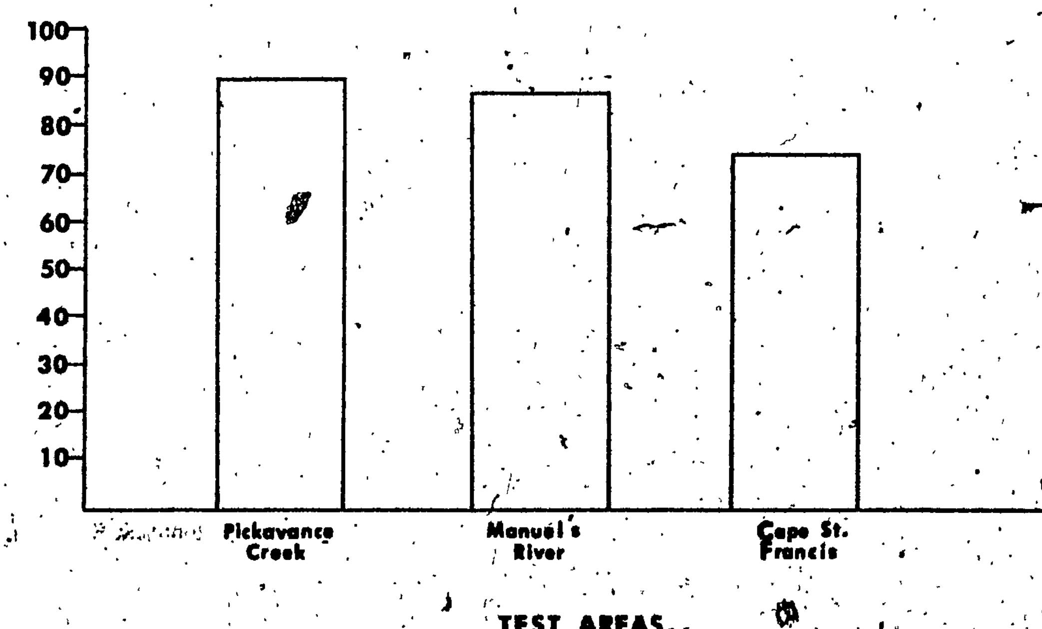
A comparison of the overall parasite prevalence of passeriform birds in the three Newfoundland test areas.

FIG. 8



PERCENT INFECTION

FIG. 9



COMPARISON OF TEST AREAS

It was shown (Table IV) in a comparison of the physical features of the test areas, that the three testing sites comprising the present study varied considerably in the yield of ornithophilic Diptera. The striking uniformity in the infection rates of the birds from the Pickavance Creek and Manuel's River area (Table VII) suggests that even with a reduced fly population in the latter area, the parasite transmission is efficient enough to produce an infection rate almost equal to the Pickavance Creek area. This point is further illustrated in Figure 9.

A significant point noted in Table VII is the low numbers of individuals of all species collected from Cape St. Francis and the correspondingly lower prevalence of blood parasites in the birds. It is especially striking when it is noted that the area is only approximately 45 km. from the Trans Canada Highway testing sites. The results, however, agree with the findings of the author in terms of the small numbers of positive ornithophilic Simulidae examined.

It is assumed that the physical and climatic conditions (particularly the continuous winds) play an important role in the situation observed in the Cape St. Francis area. The almost total absence of breeding grounds for the ornithophilic simuliids, culicids and ceratopogonids would result in a lowered prevalence of blood parasites. Bennett *et al.* (1974) state these two factors would mechanically inhibit vector-host contact and result in the lower blood parasite infection.

SUMMARY DISCUSSION

The parasite prevalence of 14,360 North American birds comprising 37 families and 163 species from many diverse and separate geographic areas of Canada and the U.S.A. is presented in this thesis (Table I). The large number of birds sampled, precludes a comparison of the overall infection rate of 55.6% with other studies of a similar size. However, the variance in the infection rates demonstrated by smaller sample sizes reported in this thesis, indicates that the parasite prevalence varies over a wide range throughout North America. Furthermore, the geographic separation of the various locations sampled and the numerous variables associated with the local environments has the effect of rendering incomparable much of the specific data on particular parasite infections.

Similarly, the prevalence of *Leucocytozoon*, *Haemoproteus* and *Plasmodium*, as determined from Table I, must be viewed as a general indication of their impact on North American bird populations. It was shown that *Leucocytozoon* and *Haemoproteus* accounted for the bulk of the infections while *Plasmodium* generally was less significant in the total bird population. Individual surveys conducted by researchers such as Bennett, Herman, Manwell, etc. on a variety of birds from different locations show that the infection rates of these parasites vary greatly. Manwell (1955) further demonstrates that the same bird species (*Turdus migratorius*) from two dissimilar locations (New York and High Rockies) possess contrasting rates of infection by the same parasite species.

Data presented on a number of bird families (Figure 2) indicates that certain families are more susceptible to infection than others. This is generally true of the passeriform birds and particularly the Icteridae, Parulidae, Fringillidae and Turdidae. It is noted that with the exception of the Fringillidae, which is shown to be equally susceptible to the three genera of hematozoa, the other bird families can attribute their infections to specific blood protozoans. The Fringillidae are known to be catholic in their habitat selection, which would undoubtedly increase their chances of becoming infected by all parasitic hematozoa.

The Anatidae, Icteridae and Fringillidae are observed as accounting for 80% of the *Haemoproteus* infection, while the major proportion of *Leucocytozoon* infection was harboured by the Parulidae, Turdidae, Tetraonidae and Fringillidae. The latter family also has the single highest incidence of *Plasmodium*. Within each of the passeriform families cited above, there were striking examples of differences among the parasite prevalence of different bird species.

As the birds represented in the North American sample vary in their nesting habitats, they were assigned their preferred natural habitat which is denoted as a function of vertical stratification. The resultant stratification demonstrated a lesser number of birds utilizing the marsh environment with the bulk of the birds preferring the woodland habitat. Consequently, the value of such a stratification of the avifauna is that it provides an insight into the levels of the forest and marsh habitats at which maximum infection occurs.

If the overall North American trend (Figure 4a) is indicative of parasite prevalence of birds in North America it is apparent that the myriad of species become infected in the mid levels of the woodland environment. This point becomes more emphatic (Table III) when it is recognized that even with 40% lesser birds preferring strata 3 than strata 1, there is an increase in the overall infection rate of approximately 25% by strata 3 over those birds which nest on the ground. It is further illustrated (Figure 4b and 4c) that this trend is confirmed for the major passerines under study as well as the remainder of the bird families excluding the passerines.

In a study which embraces such a large number of birds, it would be of tremendous value if the specific parasites could be correlated with each of the particular strata so as to have application to other surveys. However, such an endeavour, in view of the present study would be meaningless. Such a comparison would require much data on the local environments in which the birds were sampled, that unfortunately was unavailable to the author..

The areas from which birds were sampled in North America were quite different geographically and each possessed its own special biotic and abiotic characteristics, e.g. California, Massachusetts, Alaska, Florida, Maine, Arizona, Ungava, British Columbia, N.W.T., Newfoundland (insular and Labrador), Alberta, Ontario, New Brunswick, etc. Even within each of these areas the local environment varies widely. Thus, the standardization or comparison of data from such diverse geographic areas represents a colossal undertaking which extends beyond the scope of this thesis.

A major hazard which is obvious in attempting to achieve a correlation as discussed above, is the effect of comparing data on the basis of each area having equal vector potential. This assumption would be erroneous in an analysis of the North American material in this study. For instance, in areas such as the south-western U.S. or the prairies of Canada, the record of low or negative *Leucocytozoon* infection represents the unavailability of the appropriate vector. Conversely, in Newfoundland and Algonquin Park, Ontario, the high percentage of birds harbouring this genus of hematozoa suggests the presence of an environment conducive to the propagation of suitable vectors for the transmission of *Leucocytozoon*. Thus, in all areas the presence or absence of suitable breeding grounds for the vectors would be one of the essential limiting factors affecting parasite prevalence. Again this agrees with the idea that the actual blood parasites contributing to the overall parasite prevalence can only be studied at the local level.

In the Newfoundland research area the opportunity was provided to study the vector potential in the same area from which data was available on the parasite prevalence of the avifauna. A general observation on the vectors was their almost total absence from the ground level in the forest habitat and subsequently the identification of their habitat preference in the mid canopy level.

In addition to establishing that the ornithophilic Simuliidae and Ceratopogonidae were primarily restricted to the 10 - 15 ft. level in the Newfoundland forest habitat, it is shown that the most abundant vectors in the area are the Simuliidae and specifically *S. latipes*. Laboratory examination of the dissected salivary glands verified that these flies harbour sporozoites of *Leucocytozoon*. Similarly, blood fed Culicoides (*C. stilobezzoides*) were observed to harbour sporozoites of *Haemoproteus* at a rate which indicated their transmission would be considerably less than that of *Leucocytozoon*. As there were no infected hippoboscids recorded and as they were taken directly from wild birds in the field it was assumed that they are not vectors of *Haemoproteus* in insular Newfoundland. The numbers of mosquitoes that had recorded positive glands were so few that it indicated a very low *Plasmodium* incidence. With the exception of the Hippoboscidae, all other ornithophilic Diptera were observed to harbour members of the Trypanosomatidae.

A survey of the blood parasites of approximately 3000 Newfoundland birds (Bennett and Laird, 1972) shows an infection rate of approximately 90% in the passeriform birds of the Avalon Peninsula, Newfoundland. A further study (Bennett *et al.*, 1974) involving 2675 Newfoundland birds demonstrates an overall infection rate of 70% in which 92% of the infected birds harboured *Leucocytozoon*, 22% *Haemoproteus*, 17% *Trypanosoma* and 2% *Plasmodium*. Both sets of data support the observations recorded by the author in the field and laboratory, related to the abundance and infection rates of the particular ornithophilic Diptera.

The lower level of the top canopy in the woodland environment, and the relatively late emergence of ornithophilic Diptera distinguish Newfoundland's environment from other parts of North America and particularly Algonquin Park. Nevertheless certain comparisons of the incidence of parasites in different birds is possible. Clearly it is higher in birds that frequent the mid canopy and is especially noticeable in species of Parulidae. The difference in prevalence is apparent in spite of the presumed lower biting fly population in Newfoundland. The high incidence with the low fly population suggests optimal operation of other factors affecting transmission.

In conclusion, it is hoped that this study was able to draw some comparisons between the parasite prevalence of the avifauna on a borad scale (North America) which does have some application to local situations such as that observed in Newfoundland. It is fully realized, however, that the extent or degree to which the concept of stratification in the avifauna and vectors can be applied is determined by a multiplicity of factors which must be examined at the local level. Final answers and solutions to the overall problem of hematozoa in the avian population will undoubetdly unfold as more studies of this type are undertaken. However, patience and objectivity are essential factors because the area of parasitology and indeed the entire sphere of science is a complicated and ever changing one.

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