eaters (Meropidae) and cooperative breeding in hot-climate birds. Ibis 114:1–14.

GIROUX, J. F. 1985. Nest sites and superclutches of American Avocets on artificial islands. Can. J. Zool. 63:1302–1305.

GROVES, S. 1984. Chick growth, sibling rivalry, and chick production in American Black Oystercatchers. Auk 101:525–531.

LAURO, B., AND J. BURGER. 1989. Nest-site selection of American Oystercatchers (*Haematopus palliatus*) in salt-marshes. Auk 106:185–192.

MAYR, E. 1939. The sex ratio in wild birds. Am. Nat. 73:156–179.

NOL, E. 1985. Sex roles in the American Oystercatcher. Behaviour 95:232–260.

NOL, E. 1989. Food supply and reproductive performance of the American Oystercatcher in Virginia. Condor 91:429–435.

NOL, E., A. J. BAKER, AND M. D. CADMAN. 1984. Clutch initiation dates, clutch size, and egg size of the American Oystercatcher in Virginia. Auk 101:855–867.

RUSSELL, E. M. 1989. Co-operative breeding—a Gondwanan perspective. Emu 89:61–62.

SAFRIEL, U. N. 1981. Social hierarchy among siblings in broods of the Oystercatcher *Haematopus ostralegus*. Behav. Ecol. Sociobiol. 9:59–63.

SAFRIEL, U. N., M. P. HARRIS, M. DE L. BROOKE, AND C. K. BRITTON. 1984. Survival of breeding oystercatchers *Haematopus ostralegus*. J. Anim. Ecol. 53:867–877.

SIBLEY, C. G., J. E. AHLQUIST, AND G. L. MONROE, JR. 1988. A classification of the living birds of the world based on DNA-DNA hybridization studies. Auk 105:408–423.

SMITH, J. N. M. 1990. Summary, p. 593–611. *In* P. B. Stacey and W. D. Koenig [eds.], Cooperative breeding in birds: long-term studies of ecology and behavior. Cambridge Univ. Press, Cambridge, England.

STACEY, P. B., AND J. D. LIGON. 1987. Territory quality and dispersal options in the Acorn Woodpecker, and a challenge to the habitat-saturation model of cooperative breeding. Am. Nat. 130:654–676.

VAN RHIJN, J. G. 1990. Unidirectionality in the phylogeny of social organization, with special reference to birds. Behaviour 115:153–173.

WALTERS J., AND B. F. WALTERS. 1980. Co-operative breeding by Southern Lapwings *Vanellus chilensis*. Ibis 122:505–509.

ZARUDSKY, J. D. 1985. Breeding status of the American Oystercatcher in the town of Hempstead. Kingbird 35:105–113.

The Condor 94:289–292

SCARCITY OF HAEMATOZOA IN BIRDS BREEDING ON THE ARCTIC TUNDRA OF NORTH AMERICA[1]

GORDON F. BENNETT
International Reference Centre for Avian Haematozoa, Memorial University of Newfoundland, St. John's, Newfoundland, A1B 3X9, Canada

ROBERT MONTGOMERIE AND GILLES SEUTIN[2]
Department of Biology, Queen's University, Kingston, Ontario, K7L 3N6, Canada

Key words: Haematozoa; tundra; arctic; parasites; longspur; ptarmigan; redpoll; plumage color.

Despite widespread interest in documenting the blood parasites of birds (e.g. Loye and Zuk 1990), there is little information available on the haematozoa of species occurring in arctic regions. Laird (1961) reported that none of the 149 individuals of 23 bird species he sampled on Prince of Wales Island (72–74°N, 96–103°W) during one summer harbored haematozoa, but no other intensive surveys have been done of North American arctic-nesting birds. In a review of haematozoan prevalence in North American birds, Greiner et al. (1975) indicate that less than 3% of birds sampled from the "arctic barrens" (their region 6) were parasitized, but they provide no further information on the sample of birds involved in this analysis.

In this paper, we report on the haematozoa found in 276 breeding birds of 10 species sampled in the course of field studies of their behavior and ecology at four very different arctic sites. While some of these species have been sampled for haematozoa before, our samples allow us to compare haematozoa prevalence between habitat types, both within and between sites. We also discuss the implications of our findings for recent comparative analyses of parasite prevalence in relation to plumage brightness in birds (see Møller 1990).

[1] Received 24 June 1991. Accepted 27 September 1991.

[2] Present address: Department of Biology, University of Pennsylvania, Philadelphia, PA 19104.

TABLE 1. Prevalence of *Haemoproteus* (H), *Leucocytozoon* (L) and *Trypanosoma* (T) in tundra-nesting birds.

Site / Species	Total individuals		Individuals with		
	Examined	Infected	H	L	T
Sarcpa Lake					
Lagopus mutus	39	0			
Eremophila alpestris	3	0			
Calcarius lapponicus	29	0			
Plectrophenax nivalis	8	0			
Churchill					
Carduelis flammea	97	63	8	53	10
Carduelis hornemanni	19	12	0	12	2
Carduelis sp.	6	1	0	1	0
Calcarius pictus	19	3	0	3	0
Zonotrichia leucophrys	4	4	0	3	1
St. Paul Island					
Aethia pusilla	14	0			
Fort Simpson					
Cygnus buccinator	38	25	18	8	0
Total	276	108	26	80	13
Percent		39.1	9.4	29.0	4.7

METHODS

Birds were captured opportunistically in a variety of ways (mist nets, noose carpets, noose poles and potter traps), often in conjunction with other research on their behavior and ecology. All individuals were banded to facilitate later identification. Blood smears were made following the protocols of Bennett (1970). All smears were air-dried in the field and fixed in 100% ethanol within 24 hr. At the International Reference Centre for Avian Haematozoa, smears were stained with Giemsa's stain and examined for *Leucocytozoon, Trypanosoma* and microfilaria at 250× and for *Haemoproteus* and *Plasmodium* at 400× magnification. Each slide was examined until approximately 100,000 erythrocytes had been scanned. In this paper we mainly report parasite prevalence, i.e., whether or not each individual was infected with each of these taxa. Parasite intensities (i.e., infestation levels per individual bird) tend to vary seasonally and among age and sex cohorts (Weatherhead and Bennett 1991) and are thus not very useful in interspecific comparisons unless these factors can be statistically or experimentally controlled.

Most of our samples were collected at Sarcpa Lake, Melville Peninsula, Northwest Territories (68°33′N, 83°19′W) during June and July 1987–1989 and at Churchill, Manitoba (58°45′N, 94°05′W) during June and July 1989. The habitat at Sarcpa Lake is upland high arctic tundra (see Montgomerie et al. 1983 for details), more than 1,000 km north of the northern limit of trees at this longitude (Danks 1981). Churchill, on the other hand, is on the arctic treeline at the northern edge of the forest-tundra/open boreal forest vegetation zone (see Fig. 3 in Danks 1981). All birds captured at Churchill were breeding within 5 km of the Hudson Bay coast, either on relatively open tundra with scattered clumps of black spruce (*Picea mariana* (Mill.) BSP) or within the spruce stands themselves (see Jehl and Smith 1970 for habitat details).

We also report on blood samples collected in June and July 1987 from Least Auklets (*Aethia pusilla*) nesting on St. Paul Island, Pribilof Islands, Alaska (57°08′N, 170°17′W) and in July and August 1989 from Trumpeter Swans (*Cygnus buccinator*) nesting on the Mackenzie River near Fort Simpson, NWT (62°N, 122°W). These two samples permit comparison with those from related species reported elsewhere. St. Paul Island is a small oceanic island in the Bering Sea, well beyond the arctic limit of trees and tall shrubs, whereas Fort Simpson is at the southern edge of the forest-tundra/open forest vegetation zone (see Danks 1981), about 500 km southwest of the arctic treeline.

At Sarcpa Lake, Churchill and on St. Paul Island, all blood smears were taken from adult breeding birds; at Fort Simpson, they were taken from 25 adult breeders and 13 goslings. Adults of both sexes were represented in all samples except Horned Larks (females only).

RESULTS AND DISCUSSION

Sarcpa Lake, Northwest Territories. No haematozoa were found in the 79 individual birds of four species sampled at Sarcpa Lake (Table 1). Both Rock Ptarmigan (*Lagopus mutus*) and Lapland Longspurs (*Calcarius lapponicus*) were sampled during the breeding season in three different years; nine individual Rock Ptarmigan and two individual Lapland Longspurs were sampled in more than one year. Thus, the absence of haematozoa in breeding birds at this site appears to be a general phenomenon.

Forty-three individuals of the same four species also were sampled by Laird (1961) in a single season on Prince of Wales Island and no haematozoa were found there either. Horned Larks (*Eremophila alpestris*) and Rock Ptarmigan also nest south of the northern limit of trees where haematozoa have been found in their blood—36% of 50 Rock Ptarmigan from insular New-

foundland harbored haematozoa (Bennett and Inder 1972) and 13% of 23 Horned Larks from St. Bride's, Newfoundland and False River, Ungava Bay, Québec had either *Leucocytozoon* or *Haemoproteus* (unpublished data, see Greiner et al. 1975). Thus, the absence of haematozoa in these species on the high arctic tundra is not a species-specific phenomenon, but rather seems to be site-related.

The complete absence of avian haematozoa from birds nesting in high arctic regions is almost certainly due to the absence of suitable vectors (see also Laird 1961, Greiner et al. 1975), especially the various species of ornithophilic black flies (Simuliidae; see Danks 1981). The fact that haematozoa have been found in both Horned Larks and Rock Ptarmigan nesting south of the arctic treeline supports this argument. The four bird species sampled at Sarcpa Lake also winter mainly in the northern half of North America where there would be no active vectors for haematozoa in the winter. Thus, the only potential vectors for haematozoa that they might have encountered on the breeding grounds are mosquitoes (Culicidae). Mosquitoes are not particularly common at Sarcpa Lake, but it is also possible that arctic species do not act as vectors for avian haematozoa.

Churchill, Manitoba. Haematozoans were found in at least some individuals of all four passerine species sampled at Churchill (Table 1). *Leucocytozoon fringillinarum* was found in all four bird species, *Trypanosoma avium* in all but the longspur, and *Haemoproteus macropigmentatus* and *H. chloris* only in the two redpolls. Parasite intensities were low ($\leq$10 infected cells per 100,000 examined) in all birds except seven individual redpolls that had up to 500 infected cells per 100,000 examined.

Parasite prevalence was highest (63–100%) in the three species that primarily occupy treed habitats and nest mainly within the treeline: the White-crowned Sparrow (*Zonotrichia leucophrys*) and the two redpolls (*Carduelis flammea* and *C. hornemanni*; Table 1). The prevalence of haematozoa in these species at Churchill is similar to levels reported for other species from three localities within the boreal forest zone: Lac Kohlmeister, Québec (60% of 129 birds of 29 species; Laird 1961); Churchill Falls, Labrador (61% of 140 birds of 21 species; Bennett 1972); and insular Newfoundland (48% of 209 birds of 3 tetraonid species; Bennett and Inder 1972). Given the abundance of potential vectors in treed habitats at Churchill (pers. obser.), it is likely that haematozoa were picked up on the breeding grounds.

Smith's Longspurs (*Calcarius pictus*), which nest on the ground in more open forest-tundra habitats (Jehl 1968), had a significantly lower prevalence of blood parasites (16%) than each of the other three passerines sampled at Churchill (Table 1; G-tests with William's correction, $G_{adj} = 9.0–15.9$, $P < 0.01$, df = 1 in each case). Since the redpolls and White-crowned Sparrows mainly nest in or among black spruce trees (Jehl and Smith 1970), this difference in parasite prevalence suggests that even when vectors for a parasites are present in the general vicinity, microhabitat characteristics may be important in parasite transmission. Thus, the constantly windy conditions in the more open tundra sites inhabited by Smith's Longspurs probably reduces their exposure to biting flies compared to sympatric species occupying more sheltered habitats. A similar argument was made by Laird (1961) to explain the low prevalence of parasites in several Charadriiforme species when compared to sympatrically breeding species of other avian orders at Lac Kohlmeister, Québec. However, it should be noted that the Charadriidae in general are seldom infected with blood parasites—only 1.2% of individuals in this family, sampled in North America, had haematozoa (Greiner et al. 1975) and it is not known whether this is due to microhabitat or some parasite resistance in this taxon.

Fort Simpson, Northwest Territories. Twenty-five adult Trumpeter Swans (*Cygnus buccinator*) were sampled near Fort Simpson, of which 19 (76%) were infected with haematozoa: *L. simondi, H. nettionis* and *H. greineri.* At this boreal forest site, six (46%) of the 13 goslings sampled were also infected with *L. simondi* and *H. greineri,* indicating that suitable vectors for these haematozoa were present on the breeding grounds and that transmission occurred there.

The prevalence (66%; Table 1) of blood parasites in swans from Fort Simpson is similar to that observed in seven other anatid species at Goose Bay, Labrador (where 48% of 56 individuals were infected; Bennett 1972), another site within the open forest/forest-tundra zone in the boreal forest (Danks 1981). This is in sharp contrast to haematozoa prevalence recorded from Snow (*Chen caerulescens*) and Canada Geese (*Branta canadensis*) in the delta of the McConnell River, NWT (60°50'N, 94°25'W), where only 3% (21/736) of the geese examined were infected (Bennett and MacInnes 1972). The McConnell River delta is on the open tundra about 200 km north of the treeline. This suggests that the scarcity of haematozoa at the McConnell River is attributable to the absence of vectors there.

St. Paul Island, Alaska. None of the 14 Least Auklets (*Aethia pusilla*) sampled harbored any haematozoa (Table 1). This is consistent with the finding of Greiner et al. (1975) who recorded no haematozoa in four other species of alcids from the north temperate zone. We can again attribute the absence of haematozoa in the Alcidae, in general, to the absence of vectors in their nesting habitat on windy, treeless oceanic islands or at sea.

CONCLUSIONS

We conclude from this study that blood parasites are virtually absent in bird species nesting on the open tundra. Although the evidence presented here indicates that this pattern is due to the absence of suitable vectors on the treeless tundra, this hypothesis will need to be tested critically by actually sampling vectors (see Bennett 1960 for suitable methods). It is possible, for example, that tundra-nesting birds are either avoided by suitable vectors or are more resistant to parasite infection than forest-dwelling species. This seems unlikely because two species that we studied (Rock Ptarmigan and Horned Lark) have haematozoa in the boreal forest zone but not on the arctic tundra. Similarly, at Churchill, there was a striking difference in parasite prevalence across species between habitats often separated by only a few hundred meters. Thus, neither a species-specific difference in parasite resistance nor a difference in vector behavior due to climate appear to

be able to account for the scarcity of haematozoa in tundra-nesting birds.

Combined with previously published work, the results of our study suggest that birds nesting on the arctic tundra and on small oceanic islands typically lack haematozoa. Among passerine bird species, in particular, only those populations nesting on the arctic tundra have been found consistently without blood parasites.

Our results also have implications for analyses of the relation between blood parasites and plumage brightness in birds. For the past decade, there has been intense interest in the hypothesis (Hamilton and Zuk 1982) that female birds might use male plumage color as an honest signal of parasite resistance. Hamilton and Zuk (1982) predicted, and found, a positive relation between blood parasite prevalence and plumage brightness across North American passerines. Subsequent workers have found evidence both for and against this prediction (see Møller 1990 for review). Our study indicates that tundra-nesting species should not be used in any comparative tests of the Hamliton-Zuk hypothesis because inter- and intraspecific variation in plumage color in these species cannot be related to variation in parasite prevalence or intensity. Thus, plumage differences between male Horned Larks (dull), Lapland Longspurs (brighter) and Snow Buntings (brightest) as well as intraspecific variation in the plumage of both male and female Lapland Longspurs (Montgomerie, unpublished data) cannot be explained by haematozoa infestations.

Our analyses also suggest that not only the presence of vectors, but also their relative abundance in different microhabitats (see Greiner et al. 1975), may influence parasite prevalence both within and among species. Vector abundance has so far not been taken into account explicitly in tests of the Hamilton-Zuk hypothesis and could potentially account for some of the apparent correlations with plumage brightness.

We thank Jim Briskie, Karen Holder, Ian Jones, Adele Mullie and Len Shandruck for providing blood smears from their study species. This study was funded by the Canadian Wildlife Service (to Len Shandruck working at Fort Simpson) and grants from the Natural Sciences and Engineering Research Council (to GFB and RM), the Scientific Training Grants Program of Indian and Northern Affairs Canada (to RM and GS), the National Geographic Society (to Ian Jones working on St. Paul Island), the Frank M. Chapman Fund and the A. B. Kelly Fund of the Province of Québec Society for the Protection of Birds (both to GS).

LITERATURE CITED

BENNETT, G. F. 1960. On some ornithophilic blood-sucking Diptera in Algonquin Park, Ontario, Canada. Can. J. Zool. 38:377–389.

BENNETT, G. F. 1970. Simple techniques for making avian blood smears. Can. J. Zool. 48:585–586.

BENNETT, G. F. 1972. Blood parasites of some birds from Labrador. Can. J. Zool. 50:353–356.

BENNETT, G. F., AND J. G. INDER. 1972. Blood parasites of game birds from insular Newfoundland. Can. J. Zool. 50:705–706.

BENNETT, G. F., AND C. D. MACINNES. 1972. Blood parasites of geese of the McConnell River, N. W. T. Can. J. Zool. 50:1–4.

DANKS, H. V. 1981. Arctic arthropods. Ent. Soc. Can., Ottawa.

GREINER, E. C., G. F. BENNETT, E. M. WHITE AND R. F. COOMBS. 1975. Distribution of the avian haematozoa of North America. Can. J. Zool. 53:1762–1787.

HAMILTON, W. D., AND M. ZUK. 1982. Heritable true fitness and bright birds: a role for parasites? Science 218:384–387.

JEHL, J. R. 1968. The breeding biology of Smith's longspur. Wilson Bull. 80:123–149.

JEHL, J. R., AND B. A. SMITH. 1970. Birds of the Churchill region, Manitoba. Manitoba Mus. Man and Nature, Winnipeg.

LAIRD, M. 1961. A lack of avian and mammalian haematozoa in the antarctic and Canadian arctic. Can. J. Zool. 39:209–213.

LOYE, J. E., AND M. ZUK [eds.]. 1990. Ecology, behavior and evolution of bird-parasite interactions. Oxford Univ. Press, Oxford, England.

MØLLER, A. P. 1990. Parasites and sexual selection: current status of the Hamilton-Zuk hypothesis. J. Evol. Biol. 3:319–328.

MONTGOMERIE, R. D., R. V. CARTAR, R. L. MCLAUGHLIN, AND B. LYON. 1983. Birds of Sarcpa Lake, Melville Peninsula, Northwest Territories: Breeding phenologies, densities and biogeography. Arctic 36:65–75.

WEATHERHEAD, P. J., AND G. F. BENNETT. 1991. Ecology of red-winged blackbird parasitism by haematozoa. Can. J. Zool. 69:2352–2359.