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TREMATODE PARASITISM AS A POSSIBLE FACTOR IN OVER-SUMMERING OF GREATER YELLOWLEGS (*TRINGA MELANOLEUCA*)

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Abstract: The possible relationship between trematode infestation and over-summering was explored in Greater Yellowlegs (*Tringa melanoleuca*). Birds were collected throughout the year in coastal Venezuela to examine seasonal and age-related variation in digenean trematode infestations. Yellowlegs were infested with eleven digenean genera. Only four genera were common to both adults and juveniles. Adults that had recently arrived on the wintering grounds were more infested with trematodes than juveniles. By spring, this relationship changed and juveniles tended to contain more trematodes than adults, although the difference was not significant. The percentage of individuals infested by digenean trematodes increased steadily from November to April-May. There was an inverse relationship between fat loads and parasite loads of birds collected by the end of the vernal pre-migratory conditioning. Trematode infestations may cause enteritis, anemia and death of some individuals. Debilitated birds, particularly juveniles, may be unable to fatten prior to migration. Thus, trematode parasitism appears to be an important factor in over-summering behavior, at least for the Greater Yellowlegs. *Accepted 12 November 1994.*

Key words: Shorebirds, over-summering, trematode, parasite, migration, fat, body conditioning, Tringa melanoleuca, *Greater Yellowlegs, Venezuela.*

INTRODUCTION

Various hypotheses have been proposed to explain over-summering behavior (individuals remaining on wintering grounds during the boreal summer) in boreal-breeding shorebirds (see Loftin 1962, McNeil 1970a, McNeil *et al.* 1994). Most authors believe that birds that over-summer are sexually immature second-year birds, but some adults in a few species do over-summer (see McNeil *et al.* 1994). Among species known to over-summer, many individuals, perhaps a majority, do migrate to the breeding grounds and, in many cases, start breeding at the end of their first year (McNeil *et al.* 1994). Why do some individuals, second-year birds and older, over-summer at southern latitudes while other members of the same species and age classes return to the Holarctic region and breed? In over-summering shorebirds, pre-migratory moult and fattening either do not take place, or are delayed (McNeil 1970a, Johnson 1977, Johnson *et al.* 1989). The possibility of a relationship between trematode infestation and over-summering in boreal-breeding shorebirds, first suggested by McNeil (1970a), was reexamined by McNeil *et al.* (1994). Helminth infestation and acquisition of partial immunity to reinfection are suspected to explain (1) why shorebird over-summerers are mainly second-year birds, and (2) why adults also over-summer, but to lesser extent (McNeil *et al.* 1994). Based on specimens collected in northeastern Venezuela, we examine the seasonal variations in the infestation of Greater Yellowlegs (*Tringa melanoleuca*) by digenean trematodes, and compare digenean intensity in adult and juvenile hosts. Digenea are endoparasites which spend their lives in two alternate hosts, one usually a vertebrate and the other an invertebrate.

MATERIALS AND METHODS

Specimens of Greater Yellowlegs were obtained every month between November 1988 and October 1989, at Laguna de los Patos (10°25' N, 64°11' W) and Laguna de Chacopata (10°41' N, 63°46' W), two coastal lagoons located in the State of Sucre.

Host specimens were examined for digeneans in the oesophagus, proventriculus, gizzard, intestine, caeca and bursa of Fabricius, kidneys, liver, gall bladder, oviduct, air sacs, abdominal cavity, and eyes, after transportation to the laboratory, generally within half an hour of being collected. Trematodes were fixed in alcohol-formalin-acetic acid (AFA), stained in Semichon's acid carmine, and mounted in Canada balsam or Permount. They were identified mainly on the basis of keys in Yamaguti (1971) and Schell (1985). The presence of Cestoda, Nematoda, and Acanthocephala was noted, but the specimens were neither counted nor identified.

The fat content of birds was estimated using the visual quantification of subcutaneous and peritoneal fat deposits, from 0 to 4, suggested for shorebirds (McNeil 1969, 1970a) and passerines (McNeil & Carrera de Itriago 1968). Voucher host skins were preserved for age determination. Adults and juveniles were distinguished based on retention of bursa of Fabricius (McNeil & Burton 1972) and plumage characteristics, using the criteria proposed by Burton & McNeil (1976) and Prater *et al.* (1977). We classified birds into two classes: juveniles which were less than 12—13 months old, and adults which were older than 13 months (include birds in their second calendar year, i.e., born the year before the calendar year of collection).

For each particular trematode species, we use the terms prevalence, intensity, and mean intensity following Margolis *et al.* (1982): Prevalence represents the percentage of host individuals infested by the particular trematode species; intensity is the number of individuals of a particular parasite species in each infested host; mean intensity corresponds to the total number of individuals of a particular parasite species in a sample of a host species, divided by the number of infested individuals of the host species in the sample. In addition, we defined the mean intensity of the helminth community as the total number of helminths (all genera together) in a sample of a host species, divided by the number of individuals of the host species in the sample infested by any helminth genus.

RESULTS

Of the ninety-nine Greater Yellowlegs (59 adults and 40 juveniles) collected, 57.6% were infected with one to four trematode species. Table 1 gives the habitat, prevalence and mean intensity of trematode species. Eleven genera of digeneans were found.

Comparing digenean faunas of adults and juveniles. Only four genera were common both to adult and juvenile hosts. The trematode species diversity of juveniles, with 10 genera, was higher than that of adults (5 genera). Specimens of *Prosthogonimus ovatus* and specimens of *Maritrema*, *Stictodora*, *Odhneria*, and *Diplostomum* were present only in juveniles.

Adult Greater Yellowlegs start arriving in Venezuela from the boreal regions by mid-July, but the largest increase in the number of individuals takes place in October with the arrival of the bulk of juveniles (McNeil 1970a). To compare the trematode infestation of adult and juvenile hosts presumed to have been arriving or just arrived after their fall southbound flight from boreal regions, we compared the trematode intensity of adults collected in August, September and October with that of juveniles collected in September, October, and November. The time-intervals did not fully overlap because juveniles migrate south roughly one month after adults (McNeil 1970a, McNeil & Burton 1973). The intensity of the helminth community of recently arrived adults was strikingly higher than that of recently arrived juveniles. In fact, the infested

Greater Yellowlegs (18 out of a total of 26 adults) had an average of 21.1 trematodes (range: 1 to 194), while only one juvenile was infested, out of a group of 8, and that with only two parasites. In addition, if we take into account the non-infested (i.e., those having 0 parasite) as well as the infested individuals and compare the mean intensity of the infestation of the 26 adults ($\bar{x} = 14.69$) and the 8 juveniles ($\bar{x}=0.25$), the average number of trematodes in adults was significantly higher than that found in juveniles (Test of equality of the means of two samples whose variances are unequal: $t=1.9075$, d.f. = 25, $P=0.034$).

In spring, most Greater Yellowlegs leave northeastern Venezuela between the end of March and the beginning of May (McNeil 1970a). The mean intensity of the digenean community of juveniles ($\bar{x}=68.69$) collected in March, April, May and June tended to be higher than that of adults ($\bar{x}=7.00$) collected during the same interval, but the difference was not significant ($t=1.6327$, d.f. = 12, $P=0.064$), although nearly so.

Seasonal variation and pre-migratory conditioning. Fig. 1A shows that the percentage of the host individuals (adults and juveniles were pooled due to the small size of the sample) infested by digenean trematodes increased steadily from November, shortly after the arrival of juveniles, to April-May (indicated by the diagonal line showing the general trend), and even as late as July—August. A significant correlation coefficient ($r=0.963$, $P < 0.001$) between the percentage of hosts infested and time (days from November to May) indicates an increasing trend of prevalence with time. This increase is mainly due to the augmenting prevalence of *Stictodora* sp., *Mesorchis denticulatus*, *Odhneria* sp., *Harrahium halli*, *Tanaisia fedtschenkoi*, and *Prosthogonimus ovatus* (Table 2).

In northeastern Venezuela, it has been shown that Greater Yellowlegs "scheduled" for migrating north have by March a high fat load, while the birds "scheduled" for staying on the wintering grounds have a low fat content, except in mid-June, when some have a fat content almost as high as that of March—April birds "scheduled" for migration (see Fig. 1B, adapted from McNeil 1970a). McNeil & Carrera de Itriago (1968) and McNeil (1969) have shown that visual quantification of fat deposits may serve to estimate the lipid condition of passerines and shorebirds, including Greater Yellowlegs, when circumstances do not permit a fat extraction. Inasmuch as Fig. 1B shows that spring migrant Greater Yellowlegs of northeastern Venezuela

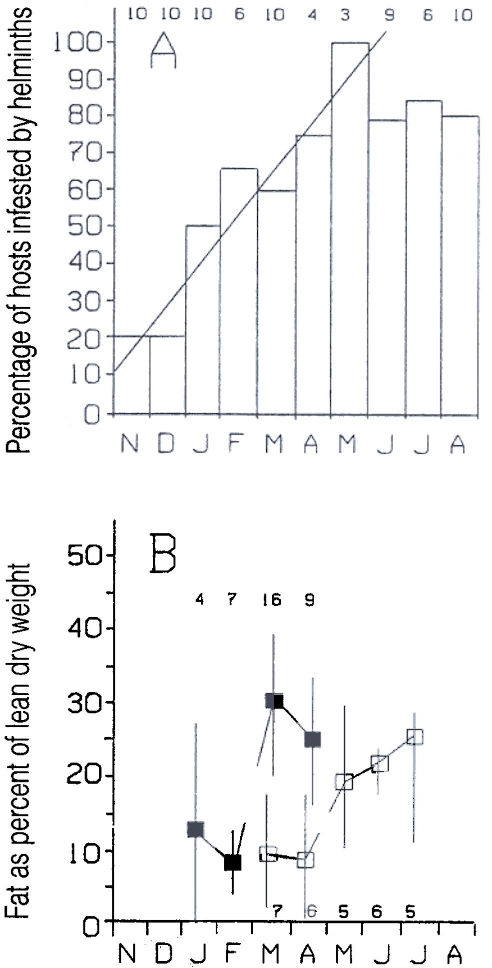

FIG. 1. Seasonal variation (A) in the percentage of Greater Yellowlegs infested by digenean trematodes in northeastern Venezuela, and (B) mean fat content ($\bar{x} \pm 95\%$ confidence limit) as percentage of lean dry mass in Greater Yellowlegs "scheduled" to undertake spring northward migration to the breeding grounds (filled squares) and "scheduled" to over-summer in northeastern Venezuela (adapted from McNeil 1970a). The diagonal line in Fig. A is hand-traced; adults and juveniles are pooled.

have their highest fat load in March, we related the visual fat scores of host specimens collected between 25 February and 17 March to their trematode intensity. As indicated by Fig. 2, there is a significant decreasing exponential relationship ($P < 0.001$), adjusted by non linear least squares (see Jolicoeur 1995), between fat loads and parasite loads ($y = ae^{-bx}$ where $a = 2.8224$ and $b = 0.0239$).

DISCUSSION

Digenean infestation and body conditioning. The detrimental effects of helminth infestation in birds are not well known. However, in humans, pathogenetic helminths depend upon the host for nourishment, produce toxic substances detrimental to the host, damage the host's intestinal mucosa, cause intestinal obstruction, have irritative and inflammatory actions, and sometimes undertake complex migrations through various host's organs (Watson 1960). Many of these detrimental effects may also apply to migratory birds, as recognized by Wehrmann (1909). For a review of suspected detrimental effects of helminths on birds, see McNeil *et al.* (1994).

Some of the digenean genera found infesting Greater Yellowlegs are known to have inimical effects on birds. For example, *Prosthogonimus* can have very serious effects. The oophoritis it causes often extends to fatal peritonitis, especially in older birds in which the young flukes enter the oviduct and develop there, after atropy of the bursa of Fabricius (Dunn 1969). Heavy infestation by members of the family Echinostomatidae, which includes *Mesorchis denticulatus*, is known to cause a severe, and occasionally fatal enteritis of hosts (Dunn 1969). The genus *Philophthalmus* is found attached to the conjunctiva under the nictitating membrane and causes lacrimation and conjunctivitis, cataract, and even blindness (Busa 1963, Penner & Fried 1963). Heavy parasitic infestation by *Diplostomum* was reported to cause loss of blood and weakness in Razorbills (*Alca torda*) (Baylis 1934).

Digenean trematodes are known to cause mortality in dabbling ducks, especially ducklings (Hoeve & Scott 1988). The damages caused by the trematodes which penetrate the intestine and enter the body cavity, then penetrate the liver and, after a period of development in the liver, leave the liver and become established in the air sacs of the avian host where they mature, can be particularly severe (McLaughlin 1977). They may cause hemopericardium, blood-filled air sacs, ruptured aorta and death of its avian

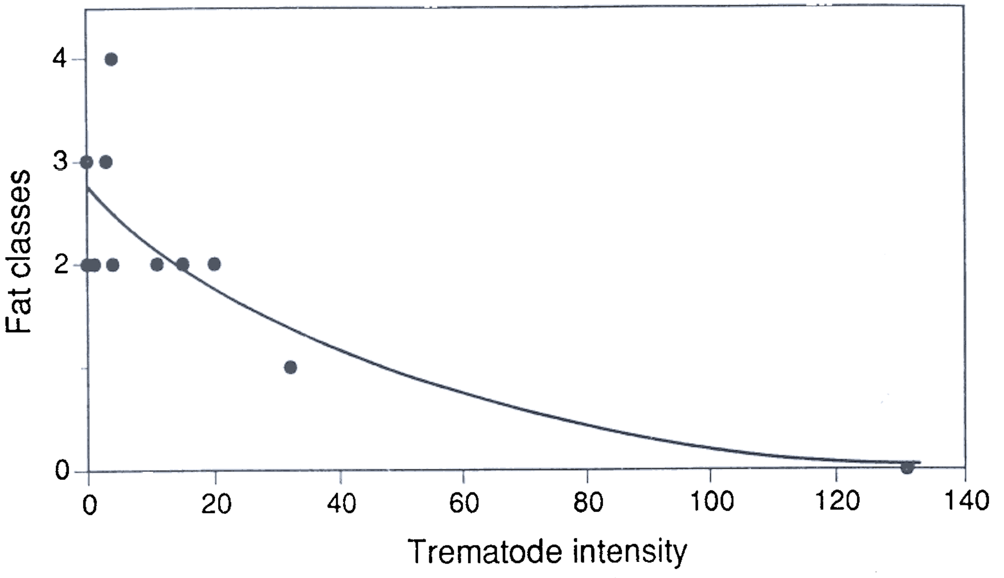

FIG. 2. Decreasing exponential relationship between fat loads and trematode intensities ($y = ae^{-bx}$) of Greate: Yellowlegs collected between 25 February and 17 March.

TABLE 1. Prevalence and mean intensity of digenean trematodes infesting Greater Yellowlegs in northeastern Venezuela.

Taxon	Habitat	Overall prevalence[1]	Mean intensity (range)[2]
Maritrema sp.	Lower intestine	2.0	1.0 (1)
Diplostomum sp.	Lower intestine	1.0	1.0 (1)
Stictodora sp.	Intestine	6.1	130.0 (17-360)
Mesorchis denticulatus	Lower intestine	19.2	22.1 (1-194)
Harrahium halli	Air sacs and body cavity	29.3	11.3 (1-61)
Odhneria sp.	Intestinal tude and caeca	5.1	43.2 (1-140)
Tanaisia fedtschenkoi	Kidneys	10.1	8.8 (1-20)
Prosthogonimus ovatus	Bursa of Fabricius	9.1	8.3 (2-20)
Uvitellina keri	Air sacs and body cavity	3.0	13.0 (5-24)
Parorchis acanthus	Cloaca	3.0	2.3 (1-4)
Philophthalmus nocturnus	Eyes, under nictitating membrane	1.0	1.0 (1)
Number of examined hosts			99
Number of hosts infested by helminths			57
Percentage of hosts infested by helminths			57.6

[1] Prevalence: Percentage of host individuals infested by the particular trematode species (Margolis *et al.* 1982). [2] Mean intensity: Total number of individuals of a particular parasite species in a sample of a host species / Number of infested individuals of the host species in the sample (Margolis *et al.* 1982).

hosts (Branton *et al.* 1985). *Harrahium halli*, the most common helminth found in the present study, probably invades air sacs and body cavities of Greater Yellowlegs in the same manner, i.e., involving perforation and lesions of the intestinal wall and/or other organs of its hosts.

Potential detrimental effects are not as clear for the intestinal parasites *Mesorchis denticulatus*, *Prosthogonimus ovatus*, *Parorchis acanthus*, and species of *Diplostomum*, *Maritrema*, *Stictodora* and *Odhneria* (Yamaguti 1971). However, the presence of even small numbers of intestinal parasites can cause the enteric environment to undergo drastic changes, resulting in disturbances in digestive, absorptive, secretory, and motor functions (Castro 1990). These conditions may contribute to local symptoms of diarrhea, steatorrhea or abdominal pain, and to systemic symptoms such as anorexia, weight loss and cachexia (Johnson 1965). Threlfall (1963) reported death due to starvation in a few shorebird species with heavy trematode infestation.

It is therefore quite possible that, in addition to causing enteritis, anemia and death of some individuals, helminths may also prevent or delay normal pre-migratory fattening in some shorebirds on their wintering grounds, and hence be an important factor responsible for their over-summering (McNeil 1970a, McNeil *et al.* 1994). Most shorebirds "scheduled" for over-summering or that actually over-summer are in full moult (McNeil 1970a, Johnson 1977, Johnson *et al.* 1989). Digestive disturbances resulting from intestinal helminth infestation would be expected to retard seasonal events such as the prebasic moult, as do poor winter feeding conditions in ducks (Richardson & Kaminski 1992). Other types of helminths (Cestoda, Nematoda, Acanthocephala) may have pathological effects sufficient to interfere in the body conditioning of shorebirds. No Nematoda or Acanthocephala were found in Greater Yellowlegs in Venezuela. However, 63.7 % of all yellowlegs (63.8% of adults and 6.6 % of juveniles) have cestodes, generally in low intensity (< 15), and mostly (36.3 %) in addition to trematodes. Nematodes and cestodes are known to parasitize shorebirds (see Canaris & Munir 1991, Schmidt & Canaris 1991, Anderson & Wong 1992).

Possible reasons for the age difference in digenean infestation. Firstly, it seems that over-summering mainly involves birds hatched the previous year (McNeil *et al.* 1994). Secondly, it seems quite clear that juvenile Greater Yellowlegs were completely, or almost completely, free of trematode infestation when they arrived on the wintering grounds after their first southward migration. Thirdly, it seems that juveniles, on tropical wintering grounds, tended to be more intensively infested with digenean trematodes than adults as spring migration approaches.

Higher infestation by endoparasites in juvenile than in adult shorebirds has also been reported elsewhere. For example, juvenile Eurasian Oystercatchers (*Haematopus ostralegus*), wintering in the Exe Estuary in UK, are more highly infested with gut helminths than adults (Goater 1989). In addition, juveniles of the same species were found to have significantly more infections with *Capillaria* sp. (Nematoda) and unidentified cestodes than adults, and were infested with a greater variety of species (Borgsteede *et al.* 1988). More intensive infestation by digenean trematodes in juveniles than in adults was also reported for ducks (Hoeve & Scott 1988).

Competition for food and feeding sites on the winter range already occupied by adults, which generally arrive several weeks earlier (McNeil 1970a), is presumably stressful for young birds (Johnson 1985). Such conditions could predispose young birds to greater impacts from parasites (O. W. Johnson, pers. comm.; see also Esh *et al.* 1975, van Riper 1991).

Birds may develop some degree of acquired immunity to reinfection with particular species of trematodes (see McNeil *et al.* 1994). Macy (1973), Huffman & Roscoe (1986), Wallace & Pence (1986), and Hoeve & Scott (1988) presented evidence for dabbling ducks suggesting that initial infections with digenean trematodes produced acquired resistance to reinfection. For more details and references concerning acquired immunity resulting from previous helminthic infestation, see Watson (1960) and Dogiel (1964).

The acquisition of partial immunity would explain, at least in part, (1) why juveniles Greater Yellowlegs tended to be more highly infested with digeneans at the time of or prior to the normal spring migration period, (2) why adults were also parasitized to some extent, and (3) why adults, which constitute the bulk of those "scheduled" for migrating north, were less infested with trematodes in spite of the fact that the heavier feeding associated with fat accumulation almost certainly exposed them to greater risk of parasitic infestation.

The differences in the trematode fauna of adults and juveniles may also be partly due to differences in foraging efficiency and diet of the two groups. It is generally recognized that juveniles have a lower foraging efficiency than adults (Recher 1966, Puttick 1979, Burger 1980, 1988, Espin *et al.* 1983, Burger & Gochfeld 1986, Goss-Custard & Durell 1987). Compared to that of juveniles, the diet of adult Greater Yellowlegs in Venezuela is expected to contain more fast moving prey, such as fishes, corixids, etc. (Robert & McNeil 1989).

TABLE 2. Seasonal variations in the infestation of Greater Yellowlegs by digenean trematodes in northeastern Venezuela, between November 1988 and October 1989.

	Prevalence percentage[1]											
	Nov.	Dec.	Jan.	Febr.	March	April	May	June	July	Aug.	Sept.	Oct.
Maritrema sp.	0	0	0	0	0	0	0	11	17	0	0	0
Diplostomum sp.	0	0	0	0	0	0	0	11	0	0	0	0
Stictodora sp.	0	0	0	0	0	0	0	33	50	0	0	0
Mesorchis denticulatus	0	0	20	0	50	50	0	22	17	10	40	30
Harrahium halli	10	10	10	33	30	50	100	44	33	60	10	40
Odhneria sp.	0	0	0	0	0	0	0	33	33	0	0	0
Tanaisia fedtschenkoi	0	10	0	16	20	0	0	22	33	0	10	10
Prosthogonimus ovatus	10	0	10	33	20	25	0	22	0	0	0	0
Uvitellina keri	0	0	20	0	25	0	0	0	0	0	0	0
Parorchis acanthus	0	0	0	0	0	0	0	0	50	0	0	0
Philophthalmus nocturnus	0	0	0	0	0	0	0	0	0	10	0	0
Number of examined hosts	10	10	10	6	10	4	3	9	6	10	10	10
Number of infested hosts by trematodes	2	2	5	4	6	3	3	7	5	8	4	7

[1] Prevalence percentage: percentage of host individuals infested by the particular trematode species (Margolis *et al.* 1982).

Environmental factors and the invasion cycle by helminths. In northeastern Venezuela, Greater Yellowlegs and other species of aquatic birds exploit seasonal lowlands which progressively dry from January to April resulting from the decrease in rainfall (McNeil 1971). In addition, large areas of mudflats and mangrove habitats used by shorebirds (including Greater Yellowlegs) in coastal lagoons progressively dry from January to April-May owing to the combined effect of the decrease in rainfall and the low-water period which lasts from January to August (see McNeil 1970a, 1971, Lefebvre *et al.* 1992a,b). During that period, many long-legged shorebird species such as the Greater Yellowlegs and the Black-necked Stilt (*Himantopus himantopus*) aggregate in the remaining wetlands and coastal lagoons (McNeil 1970b, 1971). Trematodes may normally be considered as having low pathogenicity, except when habitat conditions are such that birds can acquire heavy worm burdens (Reid 1991). Some parasite species can become a problem when crowding or flocking of many individuals of the same host species occurs (Dogiel 1964, Schmidt & Roberts 1985). Over the years, a great deal of pressure has been placed on tropical wetlands and coastal habitats, much of it at the expense of shorebirds (McNeil *et al.* 1985, 1990). Increased crowding in migratory shorebirds on the wintering grounds may lead to a more rapid contamination of shorebirds by digenean helminths through a more rapid contamination of some of their prey, the intermediate hosts, though no evidence is currently available to support this hypothesis.

CONCLUSION

It seems likely that trematode infestation may be a significant factor responsible for over-summering in at least some shorebird species, although probably not in all species. The present paper is intended to stimulate interest in the subject by parasitologists, ornithologists, and veterinarians and to raise questions for further research into the area of parasite and host interactions, including: (1) Since we know that both prevalence and intensity of trematode infestation vary from species to species, do the over-summering species represent the most parasitized ones? (2) Are those species that are not known to over-summer the least parasitized? (3) Do shorebird species that have high over-summering populations play a significant role as reservoir hosts, in contrast to species of which most or all individuals migrate to breeding grounds? (4) What role do differences in the diet and foraging efficiency of adults and juveniles play in explaining the differences regarding the trematode faunas of the two groups? One critical test would be to verify whether or not birds within one age-class that are fat and have "ready-to-go" plumage have few parasites, while the "not-ready-to-go" ones have large parasite loads. Comparison should preferably be made between birds that migrated and those which failed to do so, but such a comparison is impracticable.

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REFERENCES

Anderson, R. C., & P. L. Wong. 1992. Western Palaearctic and Ethiopian species of *Skrjabinoclava* (Nematoda: Acuarioidea) in Icelandic shorebirds (Aves: Charadriiformes) *en route* to breed in the New World and Greenland. Can. J. Zool. 70: 1861—1877.

Baylis, H. A. 1934. Fatal parasitic enteritis among Razorbills. Vet. Rec. 49: 1472—1473.

Borgsteede, F. H. M., van Den Broek, E., & C. Swennen. 1988. Helminth parasites of the digestive tract of the Oystercatcher, *Haematopus ostralegus*, in the Wadden Sea, The Netherlands. Neth. J. Sea Res. 22: 171—174.

Branton, S. L., Deaton, J. W., Gerlach, H., & M. D. Ruff. 1985. *Cyclocoelum mutabile* infection and aortic rupture in an American Coot (*Fulica americana*). Avian Dis. 29: 246—249.

Burger, J. 1980. Age differences in foraging Black-necked Stilts in Texas. Auk 97: 633—636.

Burger, J. 1988. Effects of age on foraging in birds. Acta XIX Congr. Intern. Ornithol.: 1127—1140.

Burger, J., & M. Gochfeld. 1986. Age differences in foraging efficiency of American Avocets *Recurvirostra americana*. Bird Behav. 6: 66—71.

Burton, J., & R. McNeil. 1976. Age determination of six species of North American shorebirds. Bird-Banding 47: 201—209.

Busa, V. 1963. On philophthalmosis of water fowls in Slovakia (Czechoslovakia). Helminthologia 4: 133—135.

Canaris, A. G., & N. T. Munir. 1991. Helminth parasites of the Western Sandpiper, *Calidris mauri* (Aves), from El Paso and Hudspeth Counties, Texas. J. Parasitol. 77: 787—789.

Castro, G. A. 1990. Intestinal pathology. Pp. 283-316 *in* Behnke, J. M. (ed.). Parasites: Immunity and pathology. London.

Dogiel, V. A. 1964. General parasitology (Translated from Russian by Z. Kabula). Edinburgh.

Dunn, A. M. 1969. Veterinary helminthology. Philadelphia.

Esh, G. W., Gibbons, J. W., & J. E. Bourque. 1975. An analysis of the relationship between stress and parasitism. Amer. Midl. Nat. 93: 339—353.

Espin, P. M. J., Tather, R. M., & J. Adams. 1983. Age and foraging success in Black-winged Stilts *Himantopus himantopus*. Ardea 71: 225—228.

Goater, C. P. 1989. Patterns of helminth parasitism in the Oystercatcher, *Haematopus ostralegus*, from the Exe Estuary, England. Ph.D. diss., Univ. of Exeter, Exeter.

Goss-Custard, J. D., & S. E. A. Le V. Dit Durell. 1987. Are-related effects in Oystercatchers, *Haematopus ostralegus*, feeding on mussels, *Mytilus edulis*. I. Foraging efficiency and interference. J. Anim. Ecol. 56: 521—536.

Hoeve, J., & M. E. Scott. 1988. Ecological studies on *Cyathocotyle bushiensis* (Digenea) and *Sphaeridiotrema globulus* (Digenea), possible pathogens of dabbling ducks in southern Québec. J. Wildl. Dis. 24: 407—421.

Huffman, J. E., & D. E. Roscoe. 1986. Acquired resistance in Mallard Ducks (*Anas platyrhynchos*) to infection with *Sphaeriodiotre globulus* (Trematoda). J. Parasitol. 72: 222—230.

Johnson, C. V. 1965. Malabsorption syndromes, clinical and theoretical considerations. Postgraduate Med. 37: 667—676.

Johnson, O. W. 1977. Plumage and molt in shorebirds summering at Enewetak Atoll. Auk 94: 222—230.

Johnson, O. W. 1985. Timing of primary molt in first-year Golden-Plovers and some evolutionary implications. Wilson Bull. 97: 237—239.

Johnson, O. W., Morton, M. L., Bruner, P. L., & P. M. Johnson. 1989. Fat cyclicity, predicted migratory flight ranges, and features of wintering behavior in Pacific Golden-Plovers. Condor 91: 156—177.

Jolicoeur, P. 1995. Unlinearized confidence limits for the statistical recovery of nonlinear relationships in biology. J. Theor. Biol. 172: 217—224.

Lefebvre, G., Poulin, B., & R. McNeil. 1992a. Settlement period and function of long-term territory in tropical mangrove passerines. Condor 94: 83—92.

Lefebvre, G., Poulin, B., & R. McNeil. 1992b. Abundance, feeding behavior, and body condition of Nearctic warblers wintering in Venezuelan mangroves. Wilson Bull. 104: 400—412.

Loftin, H. 1962. A study of boreal shorebirds summering on Apalachee Bay, Florida. Bird-Banding 33: 21—42.

Macy, R. W. 1973. Acquired resistance in ducks to infection with the psilostome trematode *Sphaeridiotrema globulus* (Rudolphy, 1914). J. Wildl. Dis. 9: 44—46.

Margolis, L., Esch, G. W., Holmes, J. C., Kuris, A. M., & G. A. Shad. 1982. The use of ecological terms in parasitology (report of an ad hoc committee of the American society of parasitologist). J. Parasitol. 68: 131—133.

McLaughlin, J. D. 1977. The migratory route of *Cyclocoelum mutabile* (Zeder) (Trematoda: Cyclocoelidae) in the American coot, *Fulica americana* (Gm.). Can. J. Zool. 55: 274—279.

McNeil, R. 1969. La détermination du contenu lipidique et de la capacité de vol chez quelques espèces d'oiseaux de rivage (Charadriidae et Scolopadidae). Can. J. Zool. 47: 525—536.

McNeil, R. 1970a. Hivernage et estivage d'oiseaux aquatiques nord-américains dans le nord-est du Venezuela (mue, accumulation de graisse, capacité de vol et routes de migration). Oiseau et R. F. O. 40: 185—302.

McNeil, R. 1970b. Condicionamiento fisiológico pre y post-reproductivo de *Charadrius wilsonia cinnamominus* (Ridgway) y de *Himantopus mexicanus* (Müller) en el nordeste de Venezuela. Acta IV Congr. Latin. Zool. 2: 749—760.

McNeil, R. 1971. Lean-season fat in a South-American population of Black-necked Stilts. Condor 73: 472—475.

McNeil, R., & J. Burton. 1972. Cranial pneumatization patterns and bursa of Fabricius in North American shorebirds. Wilson Bull. 84: 329—339.

McNeil, R., & J. Burton. 1973. Dispersal of some southbound migrating North American shorebirds away from the Magdalen Islands, gulf of St. Lawrence, and Sable Island, Nova Scotia. Carib. J. Sci. 13: 257—278.

McNeil, R., & M. Carrera de Itriago. 1968. Fat deposition in the Scissors-tailed Flycatcher (*Muscivora t. tyrannus*) and the Small-billed Elaenia (*Elaenia parvirostris*) during the austral migratory period in northern Venezuela. Can. J. Zool. 46: 123—128.

McNeil, R., Díaz, M. T., & A. Villeneuve. *Inpress*. The mystery of shorebird over-summering: a new hypothesis. Ardea.

McNeil, R., Limoges, B., & J. R. Rodriguez S. 1990. Corocoro colorado (*Eudocimus ruber*) y otras aves acuáticas coloniales de las lagunas, ciénagas y salinas de la costa centro-oriental de Venezuela. IWRB Spec. Publ. 11: 28—45.

McNeil, R., Ouellet, H., & J. R. Rodriguez S. 1985. Urgencia de un programa de conservación de los ambientes costeros (lagunas, planicies fangosas, laderas costeras y manglares) del Norte de América del sur. Bol. Soc. Venez. Cienc. Nat. 143: 449—474.

Penner, L. R., & B. Fried. 1963. *Philophthalmus hegeneri* sp. n., an ocular trematode from birds. J. Parasitol. 6: 974—977.

Prater, A. J., Marchant, J. H., & J. Vuorrinen. 1977. Guide to the identification and ageing of Holarctic waders. British Trust for Ornithology Guide No. 17, Tring.

Puttick, G. M. 1979. Foraging behaviour and activity budgets of Curlew Sandpipers. Ardea 67: 111—122.

Recher, H. F. 1966. Some aspects of the ecology of migrant shorebirds. Ecology 47: 393—407.

Reid, W. M. 1991. Cestodes and trematodes. Pp. 764—778 *in* Calnek, B. W. (ed.). Diseases of poultry. Ames.

Richardson, D. M., & R. M. Kaminski. 1992. Diet restriction, diet quality, and prebasic molt in female Mallards. J. Wildl. Manage. 56: 531—539.

Robert, M., & R. McNeil. 1989. Comparative day and night feeding strategies of shorebird species in a tropical environment. Ibis 131: 69—79.

Schell, S. 1985. Trematodes of North America. Univ. Moscow, Idaho.

Schmidt, G. D., & A. G. Canaris. 1992. Tapeworms of the families Progynotaeniidae Fuhrmann, 1936 and Dioecocestidae Southwell, 1930 from shorebirds of South Africa. Syst. Parasitol. 23: 37—42.

Schmidt, G. D., & L. S. Roberts. 1985. Foundations of parasitology. Toronto.

Threlfall, W. 1963. Factors concerned in the mortality of some birds which perished in Anglesey and Northern Caernarvonshire during the winter of 1963, with special reference to parasitism by helminths. Ann. Mag. Nat. Hist. 13: 721—737.

Van Riper, C. III. 1991. Parasite communities in wet and dry forest subpopulations of the Hawaii Common Amaniki. Pp. 140—153 *in* Loy, J. E., & M. Zuk (eds.). Bird-parasite interactions. New York.

Wallace, B. M., & D. B. Pence. 1986. Population dynamics of the helminth community from migrating Blue-winged Teal: loss of helminths without replacement on the wintering grounds. Can. J. Zool. 64: 1765—1773.

Watson, J. M. 1960. Medical helminthology. Baillière Tindall and Cox, London.

Wehrmann (Née Brodsky), S. 1909. Sur l'action pathogène des Helminthes des oiseaux. Archv. Parasitol. 13: 204—238.

Yamaguti, S. 1971. Synopsis of digenetic trematodes of vertebrates. Vol. 1. Keigaku Publ. Co., Tokyo.