RECURRENT, LATE-SUMMER MORTALITY OF DABBLING DUCKS IN SOUTHERN QUEBEC INDUCED BY THE DIGENEANS *Sphaeridiotrema globulus* (RUDOLPHI, 1814) AND *Cyathocotyle bushiensis* KHAN, 1962.

BY

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ABSTRACT

A recurrent, late-summer mortality of ducks was examined under the hypothesis that it was parasite-induced. Comparison of parasite infection levels in ducks found dead and in hunter-shot ducks revealed that the digeneans *Sphaeridiotrema globulus* (Rudolphi, 1814) and *Cyathocotyle bushiensis* Khan, 1962 were both significantly more prevalent in ducks found dead. The intensity of infection, however, was significantly higher in the ducks found dead only for *S. globulus*. It was concluded that the annual mortality was probably caused by heavy infections with these two parasites, but that *S. globulus* was the more important pathogen. Most duck species were equally susceptible to experimental infection with *C. bushiensis*, suggesting that interspecific differences in feeding ecology, and not differences in innate susceptibility to infection, were responsible for blue-winged teal (*Anas discors*) and black ducks (*Anas rubripes*) being most affected by the infection and mortality in the field. Measurements of parasite acquisition by sentinel ducks suggested that seasonal changes in the availability of *C. bushiensis* metacercariae to ducks were not responsible for the peak in mortality during late-summer. The mortality, instead, seemed to be correlated with an annual, pre-migration flocking behavior of ducks on the productive and infective marshes of the St. Lawrence River and/or peak transmission of *S. globulus* cercariae among freshwater snails.

ABREGE

La mortalité récurrente observée chez les canards à la fin de l'été fut examinée en supposant que tel phénomène était causé par des parasites. La comparaison du degré d'infection parasitaire entre les canards trouvés morts et ceux abattus par les chasseurs révéla l'incidence significativement plus élevée des digéniens *Sphaeridiotrema globulus* (Rudolphi, 1814) et *Cyathocotyle bushiensis* Khan, 1962 chez les canards trouvés morts. Cependant, seule l'intensité des infections à *S. globulus* fut significativement plus élevée chez les canards trouvés morts. Il a été conclut que la mortalité annuelle de canards était causée par des infections considérables avec ces deux parasites, mais que *S. globulus* était le plus important des deux pathogènes. La majorité des différentes especes de canards étudiées était également susceptible à une infection expérimentale avec *C. bushiensis*. Ceci suggère que les différences interspécifiques dans les habitudes alimentaires, et non les différences innées déterminant la prédisposition à l'infection, étaient responsables pour la susceptibilité à l'infection et la mortalité de la sarcelle à ailes bleues (*Anas discors*) et du canard noir (*Anas rubripes*) sur le terrain. L'acquisition constante de *C. bushiensis* par des canards en sentinelle suggére que les changements saisoniers dans la disponibilité des métacercaires ne correspond pas avec le sommet de mortalité observé à la fin de l'été. La mortalité semble plutôt correler avec le rassemblement des canards, précédant la migration, sur les berges fertiles et infectées du fleuve St.-Laurent, et/ou la transmission maximale de *S. globulus* parmi les escargots d'eau douce.

SUGGESTED SHORT TITLE:

PARASITE-INDUCED MORTALITY OF DUCKS

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I would like to acknowledge the Canadian Wildlife Service for providing permits to salvage duck carcasses and to hold experimental ducks. I would also like to thank all the personnel from the M.L.C.P. who co-operated by collecting duck carcasses; the interest and enthusiasm of D. Dolan was especially appreciated.

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Massive late-summer die-offs of dabbling ducks on the St. Lawrence River in southern Québec during the early and late 1960's were attributed to the digenean *Cyathocotyle bushiensis* Khan, 1962 because this parasite was consistently recovered from the ceca of ducks found dead (Gibson *et al.*, 1972). This is the only known report of *C. bushiensis* in its wild, definitive host; essentially nothing is known about the ecology of this parasite. Late-summer die-offs of ducks have continued to occur in southern Québec (R. Parent, pers. comm.; Demers, 1985).

This study had three main objectives In Chapter 1, the hypothesis that *C. bushiensis* is still responsible for the mortalities is tested by comparing infection levels in ducks found dead with infection levels in hunter-shot ducks Field data from Chapter 1 indicates that duck species are not all equally affected by the mortality Therefore, the second main objective, presented in Chapter 2, is to test whether differences in innate susceptibility to infection are responsible for the variable effect of the mortality on different duck species. Chapter 3 presents the third main objective, which is to test whether seasonal changes in the availability of metacercariae to ducks may be responsible for the regular occurrence of the mortality during late-summer.

LITERATURE CITED

DEMERS, A., 1985. A quand le retour des canards noirs? Le Bulletin des Agriculteurs 8: 74-79.

GIBSON, G.G., E. BROUGHTON AND L.P.E. CHOQUETTE, 1972. Waterfowl mortality caused by *Cyathocotyle bushiensis* Khan, 1962 (Trematoda:Cyathocotylidae), St. Lawrence River, Quebec. Can. J. Zool. 50: 1351-1356.

STATEMENT OF AUTHORSHIP

Hunter-shot ducks collected in 1982 and 1983, and "dead ducks" collected in 1983, were collected and examined by M. E. Scott. The collection of ducks in 1984 and 1985, and all other experiments, were performed by the Candidate.

"While the inclusion of manuscripts co-authored by the candidate and others is not prohibited by McGill, the Candidate is warned to make an explicit statement on who contributed to such work and to what extent, and Supervisors and others will have to bear witness to the accuracy of such claims before the oral committee. It should also be noted that the task of the External Examiner is made much more difficult in such cases, and it is in the Candidate's interest to make authorship responsibilities perfectly clear."

CHAPTER 1

A RECURRENT, LATE-SUMMER PARASITE-INDUCED MORTALITY OF DABBLING DUCKS IN SOUTHERN QUEBEC.*

BY

HOEVE, J. AND M.E. SCOTT

* for submission to the Journal of Wildlife Diseases.

ABSTRACT

A recurrent, late-summer mortality of dabbling ducks in southern Québec was examined under the hypothesis that the mortality was parasite-induced. Comparison of parasite infection levels in ducks found dead and in hunter-shot ducks revealed two digeneans, *Sphaeridiotrema globulus* (Rudolphi, 1814) and *Cyathocotyle bushiensis* Khan, 1962, which were significantly more prevalent in dead ducks than in hunter-shot ducks. However, the intensity of infection was significantly greater in dead ducks than in hunter-shot ducks only for *S. globulus*. It is believed that heavy infections with these two parasites were responsible for the mortality, but that *S. globulus* was probably the more important pathogen. The mortality was highly seasonal, as two thirds of all dead ducks were recovered during the last two weeks of August. Blue-winged teal (*Anas discors*) and black ducks (*Anas rubripes*) were the species most affected by the mortality.

INTRODUCTION

It is generally agreed that parasite-induced host mortality does occur, but whether the mortality is additive (Anderson, 1978) or compensatory (Holmes, 1982) is a matter of debate. Also of general agreement is the need for good empirical evidence of parasite-induced host mortality occurring under natural conditions. One particular area where research is needed is field studies demonstrating a correlation between intensity of parasitism and host mortality (Hassell *et al*, 1982)

In 1972, Gibson *et al.* reported that waterfowl mortalities on the St. Lawrence River, Quebec, during the early 1960's and again during 1969 and 1970 were caused by the digenean parasite *Cyathocotyle bushiensis* Khan, 1962. A late-summer mortality of dabbling ducks has recurred annually since this first published report (R. Parent, M.L.C.P. Waterfowl Biologist, pers. comm.; Demers, 1985). This seems to be an example of a parasite which, on a regular basis, kills its normal definitive host under natural conditions. It is therefore an ideal candidate for the type of field study suggested above.

The work of Gibson *et al.* (1972) is the first and only known report of *C. bushiensis* in its wild, definitive host. In their study, Gibson *et al.* (1972) examined only the carcasses of ducks found dead; nothing is known about the ecology of *C. bushiensis* in wild, free-flying duck populations.

This study had two objectives. First, we investigated the hypothesis that *C. bushiensis* is responsible for the recurrent, late-summer duck mortality by comparing infection levels in ducks found dead with infection levels in the "normal", free-flying duck population, as represented by hunter-shot ducks. Infections with other gastrointestinal helminths were also recorded, to study whether other parasites might be responsible for the mortality. Second, we examined if the mortality affected all species of ducks equally.

MATERIALS AND METHODS

"Dead ducks" include all those ducks found dead in the field with no obvious external cause of mortality. These carcasses were collected during the period from August 1983 to September 1985. Specimens were labelled as to collection site and date and then frozen. At necropsy, the species, age and sex of the carcasses were determined by cloacal and plumage characteristics (Larson and Taber, 1980; Bellrose, 1976) and the gastrointestinal tracts were removed. Examination during necropsy revealed three "dead duck" carcasses which showed evidence of hunting mortality, so these were added to the "hunter-shot duck" samples.

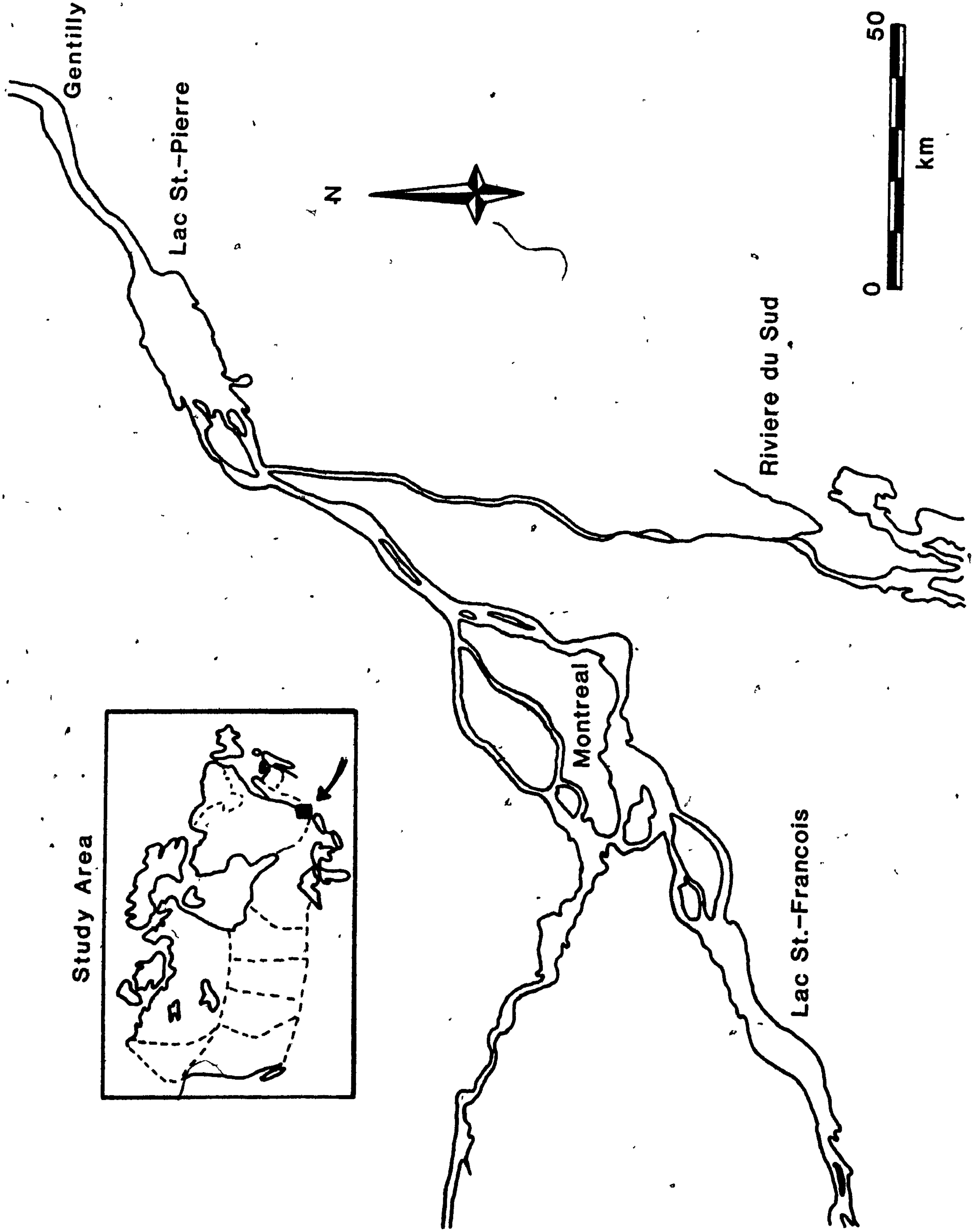
Gastrointestinal tracts of hunter-shot ducks were collected from three areas in southern Québec where duck mortality had been reported: Lac St. Pierre, Lac St. François and Rivière du Sud (Figure 1). These "hunter-shot duck" samples were collected only during the opening weekend of hunting season (mid-September) from 1982 to 1985. Each sample was labelled by species, age and sex of duck and site and date of collection, then frozen for later examination.

All intestines were examined for large helminths using a dissecting microscope (5X). Smaller helminths were recovered by washing the intestinal contents through a sieve (80 mesh/inch) and examining the residue with a dissecting microscope (10X). The gizzards of all "dead ducks" and "hunter-shot" blue-winged teal (*Anas discors*) were examined for nematodes by peeling off and examining the underside of the gizzard lining with a dissecting microscope (5X).

To quantify the worm burdens of ducks heavily infected (>500 worms) with *Sphaeridiotrema globulus* (Rudolphi, 1814), a subsampling technique was used. The washed intestinal contents were suspended in 50 ml of water and thoroughly mixed. An aliquot of approximately 2 ml was removed, the worms counted, and the number corrected to estimate the total worm burden. The accuracy of this technique was assayed by estimating the worm burden of 12 ducks by subsampling and then counting all worms individually. Spearman

FIGURE 1.

Map of southwestern Québec, showing areas on the St. Lawrence River and its tributaries where "dead duck" and "hunter-shot duck" samples were collected, 1982 - 1985. Inset shows study area on a larger scale map.


Gentilly
Lac St.-Pierre
N
0
50
km
Riviere du Sud
Montreal
Lac St.-Francois
Study Area

rank correlation analysis yielded a significant positive relationship between the two estimates (r=0.811, P<0.01; mean % difference=21.4), and it is felt that this technique provided a reliable estimate of worm burden in heavily infected ducks.

Helminths were fixed in 10% buffered formalin. Large helminths were then stored in 70% alcohol while small helminths were stained with aceto-carmine, cleared in xylene and mounted in Permount. Digeneans were identified using McDonald (1981); representative specimens have been deposited in the Parasite Collection of the National Museums of Canada (accession numbers NMCP1986-0012 to NMCP1986-0022).

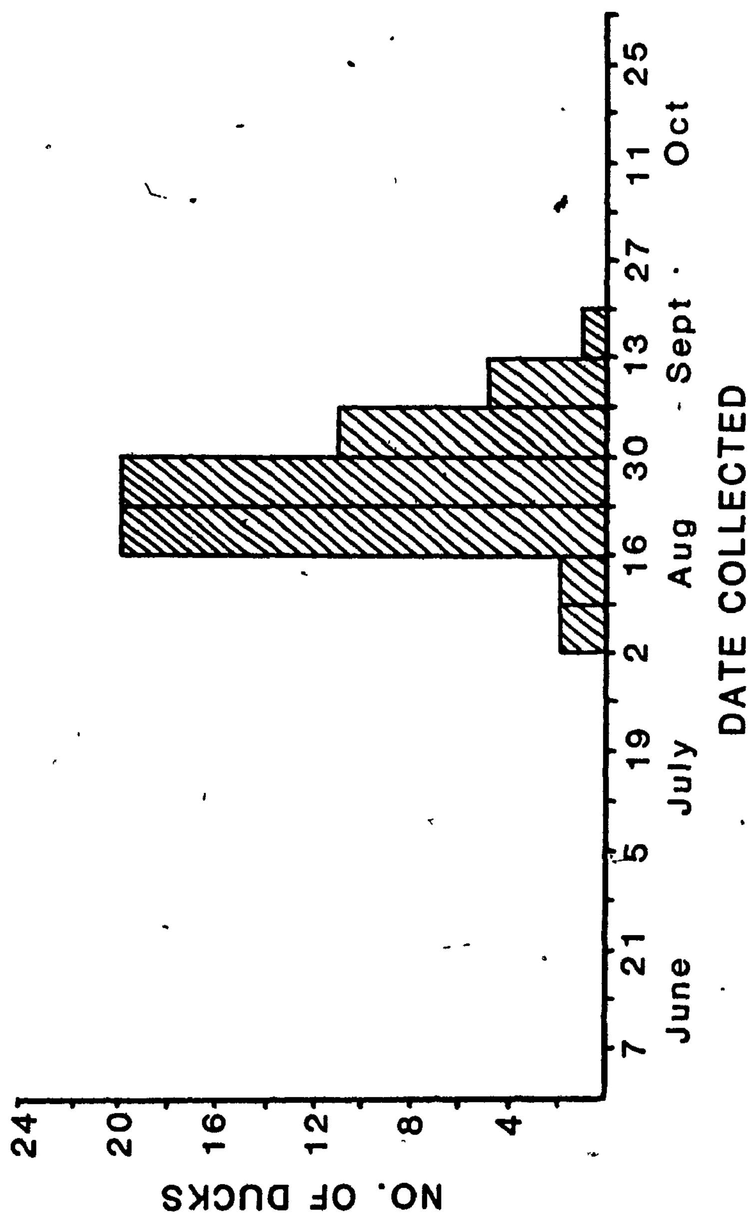
Chi-square and Fisher's exact tests were used to test for differences in prevalence between "dead duck" and "hunter-shot duck" samples. Mann-Whitney U-tests and Randomization Tests for Two Independant Samples (Siegel, 1956) were used to compare mean intensity of infection among samples, where intensity is defined as the total number of worms recovered divided by the number of infected hosts (Margolis *et al.*, 1982). Discriminant function analyses were performed using the STEPDISC procedure of the SAS statistical packages; the level of significance was set at 15% to select only the best discriminators. The species composition of the "dead duck" sample and the local duck population was compared using a G-test. Unless otherwise stated, the level of significance was set at 5%.

RESULTS

A total of 61 "dead ducks" were collected during this study. Most of the carcasses were collected from Lac St. Pierre (25) and Gentilly (28), with the remainder collected at the Rivière du Sud (3), Lac St. François (3) and around the island of Montréal (2) (Figure 1). "Dead ducks" began to be recovered early in August but two-thirds of all "dead ducks" collected were recovered during the last two weeks of August (Figure 2); the numbers declined until mid-September. One each of pintail (*Anas acuta*), gadwall (*Anas strepera*) and shoveler (*Anas clypeata*) were collected but analyses

FIGURE 2.

Seasonality of parasite-induced duck mortality, 1983 - 1985. Histogram shows numbers of "dead ducks" collected during each week beginning June 1.


NO. OF DUCKS
24
20
16
12
8
4
7
21
5
19
2
16
30
13
27
11
25
June
July
Aug
Sept
Oct
DATE COLLECTED

were restricted only to the four species most frequently collected: blue-winged teal, green-winged teal (*Anas crecca carolinensis*), mallards (*Anas platyrhynchos*) and black ducks (*Anas rubripes*) (Table 1). Therefore, only the data from these four species of "hunter-shot ducks" are presented (Table 1), although data for other species were also collected.

Generally, the helminth fauna of the two samples was similar (Table 1) but statistical comparison of the prevalences produced three noteworthy results. First, the prevalence of *C. bushiensis* in the "dead duck" samples was significantly higher than in the "hunter-shot duck" samples for all species. Second, except for green-winged teal, the prevalence of *S. globulus* was also significantly higher in the "dead duck" samples. Third, all blue-winged teal in both samples were infected with gizzard nematodes. Further analyses were restricted to these three parasites.

The mean intensity of gizzard nematode infections in "dead" blue-winged teal (9.0 worms) was not significantly different from the intensity in "hunter-shot" blue-winged teal (9.1 worms) ($H=0.6250$, $df=1$, $P>0.05$). Comparison of the intensity of infection for *C. bushiensis* and *S. globulus* (Table 2) indicated that only *S. globulus* had an intensity which was consistently greater in the "dead duck" samples compared with "hunter-shot duck" samples and, except for 1985 mallards, these differences were statistically significant. In contrast, the intensity of *C. bushiensis* was higher in "hunter-shot" black ducks than "dead" black ducks in 1985, and the intensity was virtually identical between the two samples for mallards in 1985 (Table 2); most of these differences in intensity were not statistically significant. Both of these parasites were also found in the "dead" pintail (101 *C. bushiensis* and 17,500 *S. globulus*), gadwall (73 and 10) and shoveler (114 and 11,500).

Discriminant function analyses of *C. bushiensis* and *S. globulus* worm burdens in "dead duck" and "hunter-shot duck" samples (Table 3) revealed that *S. globulus* infection level was the strongest discriminator (largest partial r^2) between the two samples for blue-winged teal, mallards and black

TABLE 1: EXAMINATION FOR SIGNIFICANTLY HIGHER PREVALENCE OF HELMINTH INFECTIONS IN "DEAD DUCK" SAMPLES THAN IN "HUNTER-SHOT DUCK" SAMPLES.

PARASITE	BLUE-WINGED TEAL					GREEN-WINGED TEAL					MALLARDS					BLACK DUCKS				
	DEAD		HUNTED			DEAD		HUNTED			DEAD		HUNTED			DEAD		HUNTED		
	n	%	n	%	diff.	n	%	n	%	diff.	n	%	n	%	diff.	n	%	n	%	diff.
Cyathocotyle bushiensis	30	100	47	31.9	***	3	100	90	4.4	***	11	72.7	211	8.1	***	14	85.7	140	18.6	***
Sphaeridiotrema globulus	30	100	35	31.4	***	3	100	43	34.9	N.S.	11	100	147	6.1	***	14	100	91	33.0	***
Notocotylus attenuatus	23	39.1	32	25.0	N.S.	2	50.0	38	7.9	N.S.	6	50.0	134	14.9	N.S.	12	16.7	85	18.8	N.S.
Zygocotyle lunata	23	13.0	32	6.3	N.S.	2	0.0	38	15.8	N.S.	6	33.3	134	43.3	N.S.	12	0.0	85	36.5	N.S.
Maritrema sp.	23	30.4	32	18.8	N.S.	2	0.0	38	5.3	N.S.	6	33.3	134	16.4	N.S.	12	0.0	85	22.4	N.S.
Psilostomatid	23	69.6	32	25.0	**	2	0.0	38	18.4	N.S.	6	33.3	134	34.3	N.S.	12	25.0	85	34.1	N.S.
Echinostoma revolutum	23	78.3	32	12.6	***	2	50.0	38	18.4	N.S.	6	83.3	134	73.1	N.S.	12	91.7	85	75.3	N.S.
Echinoparyphium recurvatum	23	8.7	32	46.9	N.S.	2	0.0	38	10.5	N.S.	6	33.3	134	50.0	N.S.	12	33.3	85	65.9	N.S.
Hypoderaeum conoideum	23	4.3	32	3.1	N.S.	2	0.0	38	0.0	N.S.	6	0.0	134	6.7	N.S.	12	0.0	85	8.2	N.S.
Levinseniella sp.	23	8.7	32	18.8	N.S.	2	0.0	38	18.4	N.S.	6	0.0	134	32.1	N.S.	12	0.0	85	37.6	N.S.
Cotylurids	23	39.1	32	59.4	N.S.	2	50.0	38	50.0	N.S.	6	50.0	134	78.4	N.S.	12	41.7	85	74.1	N.S.
Intestinal Cestodes	23	56.5	32	68.8	N.S.	2	0.0	38	76.3	N.S.	6	50.0	134	88.1	N.S.	12	41.7	85	92.9	N.S.
Gastrotaenia sp.	23	21.7	18	11.1	N.S.	2	0.0	0	-		4	0.0	0	-		4	0.0	0	-	
Acanthocephalans	23	47.8	32	62.5	N.S.	2	0.0	38	52.6	N.S.	6	50.0	134	67.9	N.S.	12	50.0	85	57.6	N.S.
Cecal Nematodes	23	56.5	32	59.4	N.S.	2	0.0	38	2.6	N.S.	6	66.7	134	55.2	N.S.	12	50.0	85	62.4	N.S.
Gizzard Nematodes	23	100	18	100	N.S.	2	50.0	0	-		4	100	0	-		4	100	0	-	

N.S. - P>0.05   * - P<0.05   ** - P<0.01   *** - P<0.001

TABLE 2: COMPARISON OF INTENSITY OF INFECTION FOR "DEAD DUCK" AND "HUNTER-SHOT DUCK" SAMPLES.

		Cyathocotyle bushiensis							*Sphaeridiotrema globulus*						
		"DEAD"			"HUNTED"				"DEAD"			"HUNTED"			
SPECIES	YR	n	$\bar{x}$	(s.d.)	n	$\bar{x}$	(s.d.)	diff.	n	$\bar{x}$	(s.d.)	n	$\bar{x}$	(s.d.)	diff.
Blue-winged Teal	1983	7	88.3	(83.8)	1	7.0	(-)	N.S.	-	-	(-)	-	-	(-)	
	1984	9	59.3	(55.1)	13	39.0	(55.7)	N.S.	9	12417.3	(9977.3)	11	2770.2	(2611.7)	***
	1985	14	19.2	(13.5)	0	-	(-)		13	4955.9	(2330.7)	0	-	(-)	
	Total	30	47.4	(56.6)	14	36.2	(54.6)	N.S.	22	8008.3	(7424.7)	11	2770.2	(2611.7)	**
Green-winged Teal	1983	1	3.0	(-)	-	-	(-)		-	-	(-)	-	-	(-)	
	1984	2	13.5	(12.0)	3	2.7	(2.9)	N.S.	2	997.5	(294.9)	15	93.4	(199.5)	*
	Total	3	10.0	(10.4)	3	2.7	(2.9)	N.S.	2	997.5	(294.9)	15	93.4	(199.5)	*
Black Ducks	1983	2	97.0	(84.9)	1	8.0	(-)	N.S.	-	-	(-)	-	-	(-)	
	1984	4	31.3	(39.6)	16	11.0	(14.4)	N.S.	5	4850.0	(3102.1)	23	282.5	(559.4)	***
	1985	6	7.5	(6.6)	4	9.8	(8.6)	N.S.	7	5245.6	(1687.0)	7	224.1	(432.7)	***
	Total	12	30.3	(46.8)	21	10.6	(12.9)	N.S.	12	5080.8	(2256.8)	30	268.9	(526.1)	***
Mallards	1983	3	27.0	(26.2)	5	2.4	(1.7)	*	-	-	(-)	-	-	(-)	
	1984	3	29.3	(26.5)	7	1.7	(1.5)	**	4	5084.0	(4896.7)	8	250.0	(368.2)	**
	1985	2	4.5	(2.1)	4	4.3	(4.6)	N.S.	2	4699.0	(1907.8)	1	412.0	(-)	N.S.
	Total	8	22.3	(22.8)	16	2.6	(2.6)	***	6	4955.7	(3892.9)	9	268.0	(348.7)	**

N.S. - P>0.05 * - P<0.05 ** - P<0.01 *** - P<0.001

TABLE 3: SUMMARY OF DISCRIMINANT FUNCTION ANALYSIS OF WORM BURDENS COMPARING "DEAD DUCK" AND "HUNTER-SHOT DUCK" SAMPLES, 1984 AND 1985.

Duck Species	Step	Variable Entered	Partial r^2	F Statistic	df
Blue-winged Teal	1	# Sphaeridiotrema	0.5726	73.691	1,55
Green-winged Teal	1	# Cyathocotyle	0.6687	86.774	1,43
Mallards	1	# Sphaeridiotrema	0.6365	264.457	1,151
	2	# Cyathocotyle	0.1520	26.878	1,150
Black Ducks	1	# Sphaeridiotrema	0.5555	126.237	1,101

ducks. Infection level of *C. bushiensis* was the strongest discriminator for green-winged teal, and it also had some discriminating power for mallards.

The high incidence of concurrent infections with *C. bushiensis* and *S. globulus* in "dead ducks" suggested that these two parasites might exhibit a positive association. Examination of concurrent infections among "hunter-shot duck" samples (Table 4) revealed that, except for wood ducks (*Aix sponsa*), the observed number of concurrent infections was consistently greater than the expected number of concurrent infections: however, none of these differences were statistically significant. Pearson product-moment correlation analyses of log-transformed ($\log_{10}(n+1)$) abundance data (number of worms/duck, including uninfected ducks) did show significant positive correlations for *C. bushiensis* and *S. globulus* in the four duck species with the highest prevalences of infection while data from mallards and wood ducks, with lower prevalences of infection, showed no significant positive correlations (Table 4).

Comparison of the species composition in "dead duck" samples and hunter bag surveys revealed that the species composition was highly significantly different between the two samples (G(Williams)=75.8778, df=6, $P<0.001$) (Figure 3). Most of the difference between the two samples resulted from the over-representation of blue-winged teal in the "dead duck" sample and the under-representation of mallards and wood ducks.

The "dead duck" sample, once divided by species, was too small to allow an analysis of the effect of host age and sex.

DISCUSSION

Samples of "hunter-shot ducks" were collected only during the opening weekend of hunting season for two reasons. First, this was the time period nearest to the late-summer die-off, and thus minimized any seasonal changes in infection levels between the two samples. Second, the species composition of the duck population present at this time most accurately reflected the species composition present during the die-off in late-summer.

TABLE 4: EXAMINATION FOR ASSOCIATION OF *Cyathocotyle* AND *Sphaeridiotrema* INFECTIONS IN HUNTER-SHOT DUCKS, 1984 AND 1985.

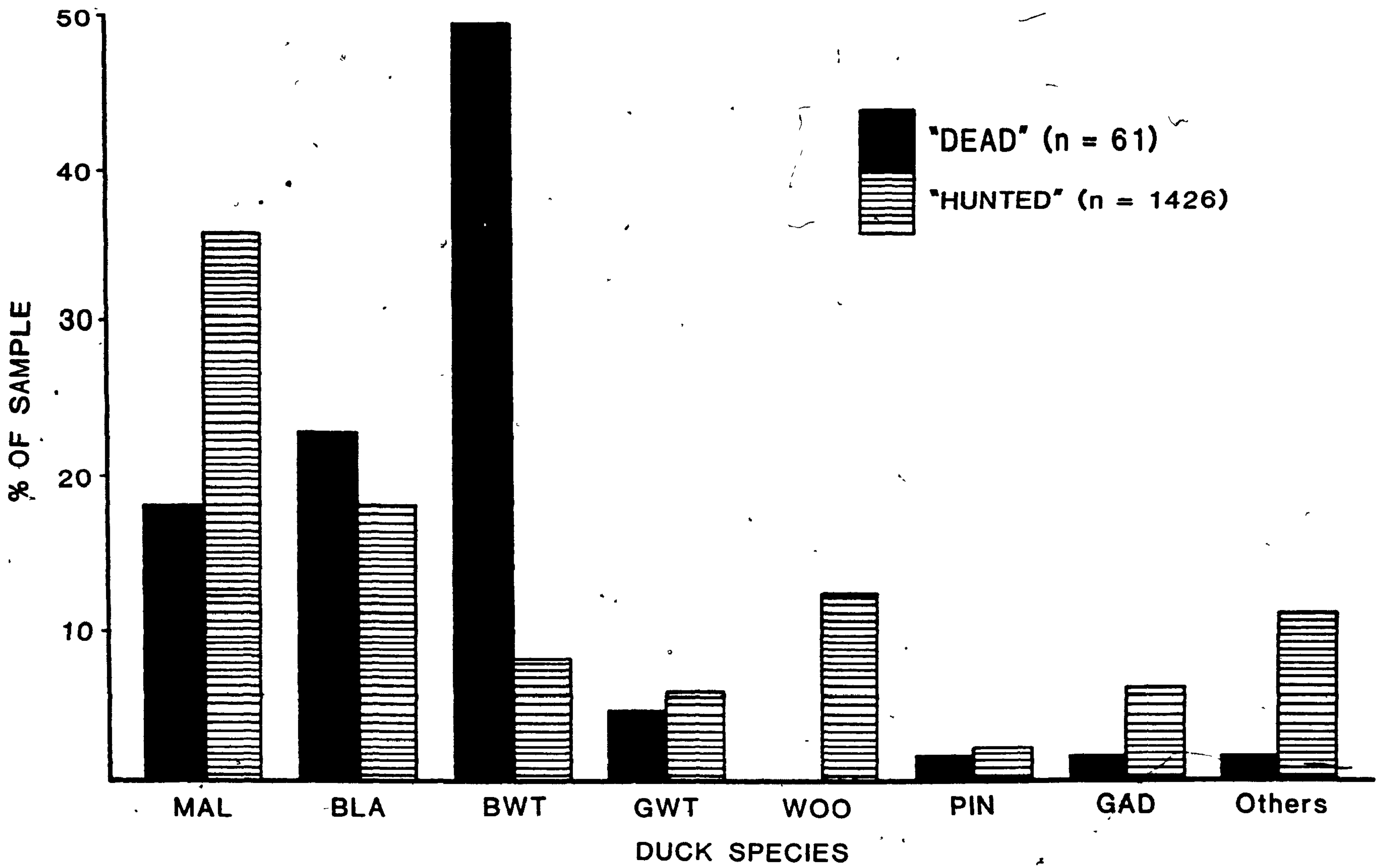
		PREVALENCE									ABUNDANCE	
		C. bushiensis		S. globulus		OBSERVED CONCURRENTLY		EXPECTED CONCURRENTLY[1]				
SPECIES	n	# Infected	%	# Infected	%	# Infected	%	# Infected	%	Diff.	Correlation Coeff.	(Sign.)
Blue-winged Teal	35	13	37.1	11	31.4	9	25.7	4	11.6	N.S.	.729	**
Green-winged Teal	43	3	7.0	15	34.9	3	7.0	1	2.4	N.S.	.483	**
Mallard	147	11	7.5	9	6.1	3	2.0	1	0.5	N.S.	.147	N.S.
Black Duck	91	21	23.3	30	33.0	11	12.1	7	7.8	N.S.	.621	**
Wood Duck	60	2	3.3	5	8.3	0	0.0	0	0.2	N.S.	-.044	N.S.
Pintail	9	3	33.3	3	33.3	3	33.3	1	11.1	N.S.	.868	**

1 - calculated as : (proportion infected with C. bushiensis) X (proportion infected with S. globulus) X n.

N.S. - P>0.05   * - P<0.05   ** - P<0.01

FIGURE 3.

Comparison of species composition between "dead duck" sample and local duck population as represented by hunter bag surveys. "Hunted" ducks includes data from opening weekend of hunting season on Lac St. Pierre from 1982 - 1984 (Dolan, 1984) plus Rivière du Sud and Lac St. François in 1984 (this study, unpubl. data). MAL=mallard, BLA=black duck, BWT=blue-winged teal, GWT= green-winged teal, WOO=wood duck, PIN=pintail, and GAD=gadwall. Data for "other" species are presented here but were not included in the analysis.


"DEAD" (n = 61)
"HUNTED" (n = 1426)
% OF SAMPLE
50
40
30
20
10
MAL
BLA
BWT
GWT
WOO
PIN
GAD
Others
DUCK SPECIES

Most of the "dead ducks" examined by Gibson *et al.* (1972) were collected from the marsh at Gentilly, while a few were collected from Lac St. François and around the island of Montréal. Many of the "dead ducks" collected during this study were recovered from these same areas, with additional carcasses collected from the islands in Lac St. Pierre and from the Rivière du Sud.

During this study, two thirds of the "dead ducks" were collected during the last two weeks of August. Gibson *et al.* (1972) reported that, during the die-offs in the early and late 1960's, many of the "dead ducks" were collected during late-summer, although some carcasses were collected as early as late-June. The probability of some duck carcasses being found and reported may increase during late-summer as the number of hunters building and repairing duck hunting blinds increases. However, many specimens from the "dead duck" sample were collected by government biologists and technicians who spent the entire summer working in the field, and these specimens were only collected during late-summer. Therefore, it is believed that the late-summer die-off is biologically real and not a result of sampling bias. Hoeve (Chapter 3) has shown that the timing of the mortality seems to be correlated with an annual, pre-migration gathering of large flocks of ducks on the productive marshes of the St. Lawrence River.

For a parasite to be implicated as the cause of the observed annual mortality, it must be present in the "dead ducks". Because ducks may die from factors other than parasites, it may be unrealistic to expect 100% of "dead ducks" to be infected with parasites; however, if parasites are the major cause of the mortality, parasite prevalence should at least approach 100%. Gibson *et al.* (1972) reported that almost all "dead ducks" collected from the St. Lawrence River were infected with *C. bushiensis*, and they concluded that the parasite was responsible for the mortality. In this study, 91.8% of the "dead ducks" were also infected with the same parasite, providing support for the hypothesis that the mortality is caused by *C. bushiensis*. Examination of the "dead ducks" for the presence of other gastrointestinal helminths revealed two other prevalent parasites: *S. globulus* and gizzard nematodes. Every one of the 61 "dead ducks" examined in this study was infected with *S. globulus*. Similarly, every blue-winged teal examined was infected with gizzard nematodes; other species of "hunter-shot ducks" were not examined for these parasites. "Gizzard nematodes" is actually a complex of, potentially, 19 genera of nematodes found in the gizzard (McDonald, 1974), and this may explain why previous parasite surveys of blue-winged teal have reported lower prevalences for the individual genera and species of gizzard nematodes (Buscher, 1966; Turner and Threlfall, 1975; Shaw and Kocan, 1980) while combined prevalences for all "gizzard nematodes" may add up to 100% or more (Buscher, 1966; Turner and Threlfall, 1975). Based on prevalence data alone, these two parasites must also be considered as potential causes of the duck mortality.

The prevalence alone of helminths, however, is not sufficient evidence for the implication as the cause of mortality. Parasite-induced host mortality is generally believed to be some function of worm burden (Keymer, 1982; Anderson and Gordon, 1982; Hassell *et al.*, 1982). Therefore, intensity of infection must also be considered. As mentioned above, gizzard nematodes were present in every blue-winged teal examined, but the mean intensity was almost identical for both the "dead duck" and the "hunter-shot duck" samples. This suggests that gizzard nematodes are very prevalent parasites of waterfowl in Québec, but there is no evidence that they are responsible for the mortality. Although the intensity of *C. bushiensis* tends to be higher in the "dead duck" samples, this difference is not consistently observed; furthermore, most of the observed differences are not statistically significant. In contrast, the intensity of *S. globulus* infections is consistently much higher in the "dead duck" samples than in the "hunter-shot duck" samples, and most of these differences are highly significant.

The worm burden of *S. globulus* is the strongest discriminator between the "dead duck" sample and the "hunter-shot duck" sample for blue-winged teal, mallards and black ducks. This is to be expected because the intensity of infection is significantly greater for the "dead duck" samples for these species. For mallards, there are also significant differences between the two samples for the intensity of *C. bushiensis* infection; therefore, worm burden of *C. bushiensis* also has some discriminating power for mallards, although much less than does *S. globulus*. The discriminating power of *C. bushiensis* worm burden for green-winged teal probably results from the low prevalence of *C. bushiensis* in "hunter-shot" green-winged teal. Because most of the "hunter-shot" green-winged teal were uninfected, and two of the three infected ducks harboured only one *C. bushiensis*, this parasite was the strongest discriminator, despite the fact that the remaining infected "hunter-shot" green-winged teal harboured more *C. bushiensis* than one of the two "dead" green-winged teal. In contrast, the two samples of green-winged teal could be completely separated based on the worm burden of *S. globulus*; worm burdens in "dead" green-winged teal were, without exception, greater than in "hunter-shot" green-winged teal, and yet the worm burden of *S. globulus* was not a significant discriminator.

Based on experimental infections (Khan, 1962; Erasmus and Ohman, 1963; Gibson *et al.*, 1972), *C. bushiensis* is capable of killing heavily infected ducks. However, the only known report of mortality caused by natural infections with *C. bushiensis* is that of Gibson *et al.* (1972). In contrast, natural infections with *S. globulus* have been reported to be fatal in ducks (Price, 1934; Cornwell and Cowan, 1963; Campbell and Jackson, 1977), coots (Trainer and Fischer, 1963) and swans (Speckman *et al.*, 1972; Roscoe and Huffman, 1982; Roscoe and Huffman, 1983). The pathogenicity of *S. globulus* has also been demonstrated experimentally in domestic ducklings infected with as few as 250 (Burns, 1961) or 1000 metacercariae (Macy, 1973), and in domestic chicks infected with 2 to 30 metacercariae (Huffman *et al.*, 1984). Based on the significant differences in both prevalence and intensity of infection, on the strength of its discriminating power, and on the numerous references to its pathogenicity, *Sphaeridiotrema globulus* seems to be the more important cause of most of the late-summer, parasite-induced duck mortality in southern Québec during recent years.

Sphaeridiotrema globulus was present less than 200 Km to the west in the Rideau River drainage before 1972 (Speckman *et al.*, 1972) and it was present about 550 Km to the south in New Jersey since at least 1970 (Roscoe and Huffman, 1982). However, *S. globulus* was not recovered from the ducks found dead in southern Québec in the late 1960's (Gibson, pers. comm.). The mean intensities of *C. bushiensis* infections recorded during this study for blue-winged teal (47.4 worms/duck) and black ducks (30.3) are considerably less than the mean intensities reported during the epizootics of the late 1960's, 260 and 180 worms/duck respectively (Gibson *et al.*, 1972). It would appear that since the late 1960's, *S. globulus* has become established in southern Québec and has become an important factor in the late-summer duck mortality.

If *S. globulus* is the more important cause of the mortality, then why is the prevalence of *C. bushiensis* significantly higher in the "dead duck" samples than in the "hunter-shot duck" samples? There are at least two possible explanations for this. First, *C. bushiensis* may still be a necessary factor in the mortality, and death is caused by the combined *C. bushiensis* and *S. globulus* infection. However, there are reports that each parasite is capable of causing host mortality independently of the other (Price, 1934; Gibson *et al.*, 1972; Campbell and Jackson, 1977), indicating that their combined presence is not a necessary prerequisite to mortality. Alternatively, their regular co-occurrence in "dead ducks" may simply be the result of simultaneous acquisition. *Bithynia tentaculata* (Gastropoda: Prosobranchia) is the only species of snail known to act as first or second intermediate host for *C. bushiensis* in southern Québec (Gibson *et al.*, 1972; Ménard, in preparation). *Sphaeridiotrema globulus* is also able to use *B. tentaculata*, among other species of snails, as both first and second intermediate host (Huffman and Fried, 1983). Therefore, ducks consuming *B. tentaculata* can acquire *C. bushiensis* and *S. globulus* infections simultaneously. Analysis of the abundance of both parasites in "hunter-shot ducks" revealed significant positive associations in four species of ducks (blue-winged teal, green-winged teal, black ducks and pintails) which had high prevalences of infection whereas worm burdens in two duck species with lower prevalences of infection (mallards and wood ducks) failed to show any association. The high prevalence of *C. bushiensis* in the "dead duck" samples therefore probably results from simultaneous acquisition of the metacercariae; although not necessary to cause mortality, once present, *C. bushiensis* is undoubtedly a contributing factor in the duck mortality.

To examine for differential mortality among duck species, the proportion that each duck species comprised in the "dead duck" sample was compared with each species' composition in the local duck population. The species composition of the local duck population is represented by hunter bag checks surveyed from 1982 to 1984, in areas where duck mortality has occurred. Such a representation will certainly include some biases. For example, hunters may selectively shoot larger ducks, so that mallards and black ducks might be over-represented in hunter bag surveys while teals might be under-represented. However, few hunters in this region of southern Québec shoot their limit (pers. obser.) and the mean success rate for hunters on Lac St. Pierre from 1982 to 1984 was consistently below three ducks per hunter (Dolan, 1984) when the bag limit was six, suggesting that hunter selection is not an important bias. A more important bias is the fact that blue-winged teal are known to be early fall migrants (Bellrose, 1976) and may therefore be under-represented in hunter-bag surveys. Nevertheless, hunter bag surveys are the best available representation of the local duck population. The comparison of samples showed that blue-winged teal were highly over-represented in the "dead duck" samples. Although, at 8%, the composition of blue-winged teal in the hunter-bag surveys is probably underestimated, the composition locally does not approach 50%, which is the composition of blue-winged teal in the "dead duck" sample. Therefore, the over-representation of blue-winged teal in the "dead duck" sample is probably a biologically real phenomenon and not solely a result of sampling bias. Examining the sample comparison for all species, it is believed that it accurately represents biologically real differences among duck species in their relative susceptibility to the late-summer mortality. Blue-winged teal was the duck species most susceptible to the mortality, followed by black ducks which were slightly over-represented in the "dead duck" samples. Similarly, Gibson *et al.* (1972) reported that black ducks and blue-winged teal were the duck species most frequently found dead in the late 1960's. All other species of duck are under-represented in the "dead duck" sample in this study. Wood ducks, in particular, are under-represented; although they are the species third most commonly shot by hunters, not one "dead" wood duck has been collected. This differential susceptibility seems to result from different feeding ecologies of the duck species; those species consuming more aquatic snails are more susceptible to the mortality (Hoeve, Chapter 2).

Late-summer deaths of dabbling ducks on the St. Lawrence River during the early and late 1960's were attributed to *C. bushiensis* (Gibson *et al.*, 1972). Since that time, however, *S. globulus* has become established in southern Quebec and it is probably this parasite which was the more important cause of the mortality during this study period. This is not to suggest that every "dead duck" died as a result of *S. globulus* infection. Some deaths may have resulted from heavy infections with *C. bushiensis*, but most deaths were probably the result of the combined infection with both parasites. Although the mortality of the ducks in this study is believed to be parasite-induced, there are undoubtedly additional waterfowl deaths each year completely unrelated to parasite infections. Hassell *et al.* (1982) suggested that field studies should try to demonstrate correlations between intensity of parasitism and host mortality. This study clearly demonstrates such a correlation for *S. globulus*, although the host mortality is complicated by the regular presence of *C. bushiensis*. Research investigating the interaction of these two pathogenic parasites and examining the patterns of acquisition would be useful.

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CONNECTING STATEMENT

In Chapter 1, it was shown that a recurrent late-summer mortality of dabbling ducks in southern Québec was probably the result of heavy infections with the digeneans *Sphaeridiotrema globulus* and *Cyathocotyle bushiensis*. It was also shown that duck species have different prevalences and intensities of infection with these two parasites, and that all duck species are not proportionally represented in the "dead duck" samples. Blue-winged teal and black ducks have the highest levels of infection, and both species are over-represented in the "dead duck" samples.

The different levels of infection among duck species may result from different exposures to the metacercariae based on feeding ecology, from differences in innate susceptibility to infection with the parasites, or from a combination of both these factors. The easiest of these hypotheses to test is to examine for innate differences in susceptibility to experimental infection. In Chapter 2, experimental infections with *C. bushiensis* were used to determine to what extent innate differences in susceptibility to infection could account for both the different levels of infection encountered among wild duck species and the disproportionate species representation in the "dead duck" samples.

CHAPTER 2

VARYING SUSCEPTIBILITY OF DUCK SPECIES TO PARASITE-INDUCED MORTALITY.*

BY

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* for submission to the Journal of Wildlife Diseases.

ABSTRACT

To determine if innate differences in susceptibility to infection with the digenean *Cyathocotyle bushiensis* Khan, 1962 could explain observed differences among duck species in terms of prevalence and intensity of infection, as well as disproportionate species representations among carcasses recovered during late-summer parasite-induced die-offs, three age classes and seven species of ducks were infected with equal numbers of metacercariae. Worm recovery on Day 7 post-infection was significantly higher for ducklings than for juveniles and adults. Worm recovery was significantly lower for wood ducks (*Aix sponsa*) than for the other species of dabbling ducks (*Anas* spp.) and lesser scaup (*Aythya affinis*). It is suggested that differences in exposure to metacercariae are responsible for the different infection levels and the disproportionate species representation in the sample of dead ducks. Thus, duck species consuming more of the intermediate host aquatic snail are more heavily infected and more frequently found dead. Three forms of cecal pathology were measured in the experimentally infected ducks. The area affected by hemorrhagic spots, pathology produced directly by the parasite on the cecal wall, was similar among all species of ducks. The area affected by plaque formations and the extent of core formations, both host-induced pathologies, did show significant differences among species, but these differences did not show a strong correlation with species' susceptibilities to mortality.

INTRODUCTION

The digenean *Cyathocotyle bushiensis* Khan, 1962 was reported to be responsible for mass die-offs of dabbling ducks on the St. Lawrence River during the late 1960's and early 1970's; black ducks (*Anas rubripes*) and blue-winged teal (*Anas discors*) were the species most frequently found dead (Gibson *et al.*, 1972). Late-summer die-offs of ducks have continued to occur in southern Québec since that time (R. Parent, Waterfowl Biologist, pers. comm.; Demers, 1985). Hoeve (Chapter 1) reported that another digenean *Sphaeridiotrema globulus* (Rudolphi, 1814) was probably the major cause of the mortalities in the years 1983 to 1985, but that *C. bushiensis* may still contribute to the mortalities. Field data showed that duck species differ in levels of infection and in proportional representation in "dead duck" samples, so that blue-winged teal and black ducks were the species most affected by the mortality in the mid-1980's (Hoeve, Chapter 1).

Infection with *C. bushiensis* can produce extensive pathology in the ceca of ducks (Khan, 1962; Erasmus and Ohman, 1963; Gibson *et al.*, 1972). However, the role that this pathology plays in causing duck mortality is unknown.

In this study, experimental infections with *C. bushiensis* were used to determine whether innate differences in susceptibility to infection were responsible for duck species being differentially affected by the recurrent parasite-induced mortality. Similarly, ducks of various ages (duckling, juvenile and adult) were also examined for differences in innate susceptibility. Gross cecal pathology was measured in these experimentally infected ducks to examine for differences between species that could be correlated with the mortality.

MATERIALS AND METHODS

All ducks were obtained from the suppliers as ducklings and were reared in the lab; thus, they were free from helminth infections. Water and commercial, non-medicated 18% poultry laying mash (Coopérative du Québec, Ste.-Rosalie, Québec) feed were supplied *ad libitum*. Ducks were classified into three age groups for this study. Ducklings included downy or partially feathered birds up to about 6 weeks of age (Class I and II ducklings of Gollop and Marshall, 1954). Adults were birds in or beyond the post-juvenile molt (Karstad and Sileo, 1971), generally greater than 4 months of age. Juveniles included ducks between 6 weeks and 4 months of age, generally about 3 months old at the time of infection. For the comparisons between species, mallards (*Anas platyrhynchos*), call ducks (domestic mallards), black ducks, pintails (*Anas acuta*), gadwalls (*Anas strepera*), blue-winged teal, wood ducks (*Aix sponsa*) and lesser scaup (*Aythya affinis*) were used.

Metacercariae were obtained from naturally infected *Bithynia tentaculata* (Gastropoda: Prosobranchia) collected at the Riviere du Sud (45°6'N; 73°14'W) and at Lac St. François (45°2'N; 74°30'W) in southern Québec. Snails were crushed in mass, washed through a course sieve (40 mesh/inch) and the metacercariae were collected on a fine sieve (120 mesh/inch), a modification of the technique described by Gibson *et al.* (1972).

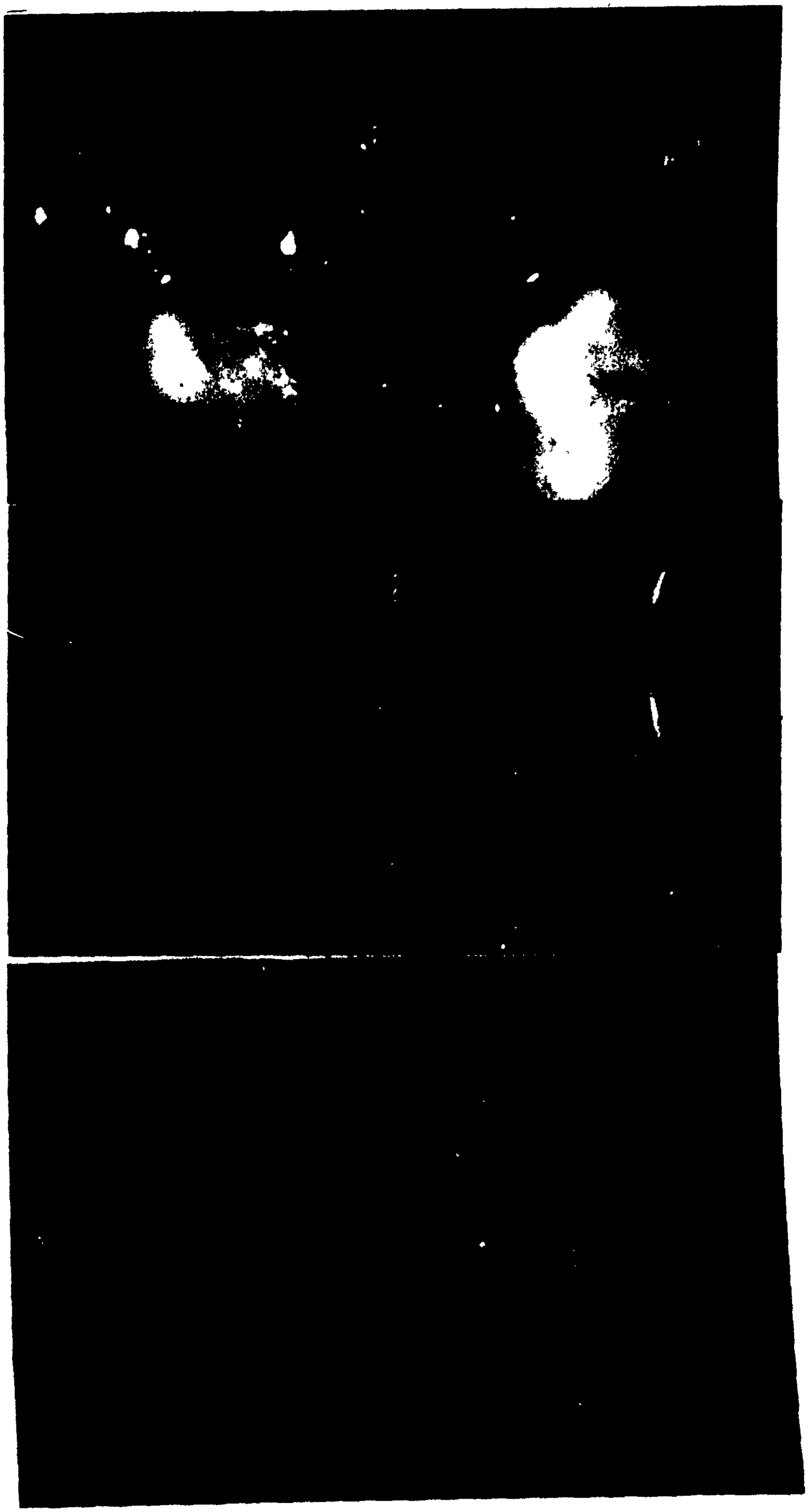
Ducks were infected, by intubation, with 25 metacercariae. Only thick-walled, supposedly "mature" metacercariae (Gibson *et al.*, 1972) were used. After infection, ducks were maintained separately in 63 X 46 X 38 cm rabbit cages, with water and feed supplied *ad libitum*.

Ducks were killed on Day 7 post infection (p.i.). Feed was removed from the cages 2 hours before sacrifice to allow the intestinal tracts to empty, thus facilitating the examination for worms. The ceca, colon and terminal section of the small intestine (equal in length to the ceca) were examined for *C. bushiensis* as described in Hoeve (Chapter 1). Only the terminal section of the small intestine was examined because no *C. bushiensis* were found in the anterior small intestine at the worm burdens used for these experiments (Scott, unpubl. data).

Three measures of gross pathology of the ceca (Figure 1) were recorded.

FIGURE 1.

Photographs of the three types of pathology measured. A: hemorrhagic spots created at the site of attachment and feeding of *Cyathocotyle bushiensis*. Notice that the spots, indicated by arrow, are the same size and shape as the adult worms. B: plaque formations, caseous fibrin secretions lining the cecal wall at previous hemorrhagic spots. Seven adult *C. bushiensis* in petri dish at right. C: core formations, fibrin secretions occupying part or all of the cecal lumen. 19 adult *C. bushiensis* in petri dish at right.



A

B

C

"Hemorrhagic spots" were the sites where *C. bushiensis* had been recently attached and feeding (Erasmus and Ohman, 1963). "Plaque formations" were caseous secretions attached to the wall of the ceca (Gibson *et al.*, 1972). "Cores", apparently of fibrin and blood (Gibson *et al.*, 1972), were secretions occupying part or all of the cecal lumen. To quantify the extent of hemorrhagic spots and plaque formations, affected ceca were gently pressed under a plexiglass plate and a dotted acetate sheet (7.8 dots/sq. cm) was superimposed over the plate. The numbers of dots covering hemorrhagic spots, plaque formations and unaffected cecal wall were counted and these were presented as both absolute area affected and as % of the total area of each cecum. Both measures were corrected for number of worms. Core development was measured by weighing the cores to the nearest 0.1 gram. The core formation measurements were adjusted to correct for number of worms and to correct for number of worms plus size of the cecum (surface area).

Kruskal-Wallis tests were used for all comparisons of experimental infections. Spearman's rank correlation analysis (Zar, 1974) was used for the analysis of feeding ecology. The level of significance was set at 5%.

RESULTS

Mallards were used to measure the effect of host age on worm establishment. Worm burden on Day 7 p.i. was significantly greater ($H=9.7450$, $df=2$, $P<0.01$) in ducklings than in juveniles or adults (Figure 2). There was no significant difference between juveniles and adults ($H=2.2361$, $df=1$, $P>0.05$).

In the experiment to determine the effect of host species on worm establishment, juvenile ducks were used whenever possible; however, 8 of the 15 blue-winged teal and all of the call ducks were adults. Four gadwalls were infected but were not included in the analysis because of the small sample size. Worm establishment was significantly lower ($H=25.7332$, $df=6$, $P<0.001$) in wood ducks than in the remaining species (Figure 3). There were

FIGURE 2.

Effect of duck age on the recovery of *Cyathocotyle bushiensis* on Day 7 p.i. Sample size equals 20 ducks for each age class. All ducks were infected with 25 metacercariae. dklg=duckling, juv=juvenile.

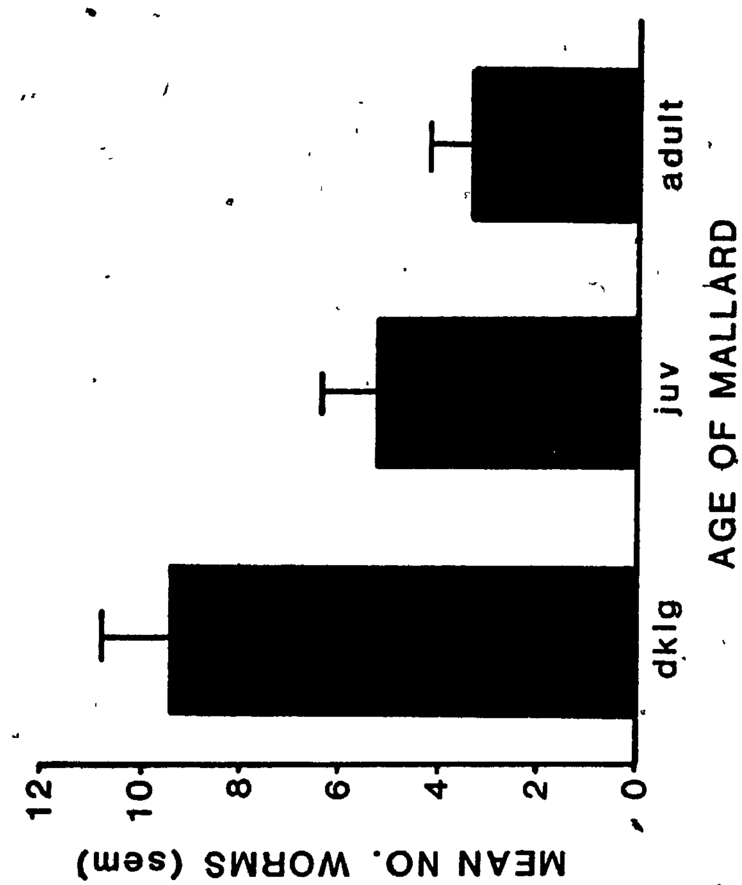
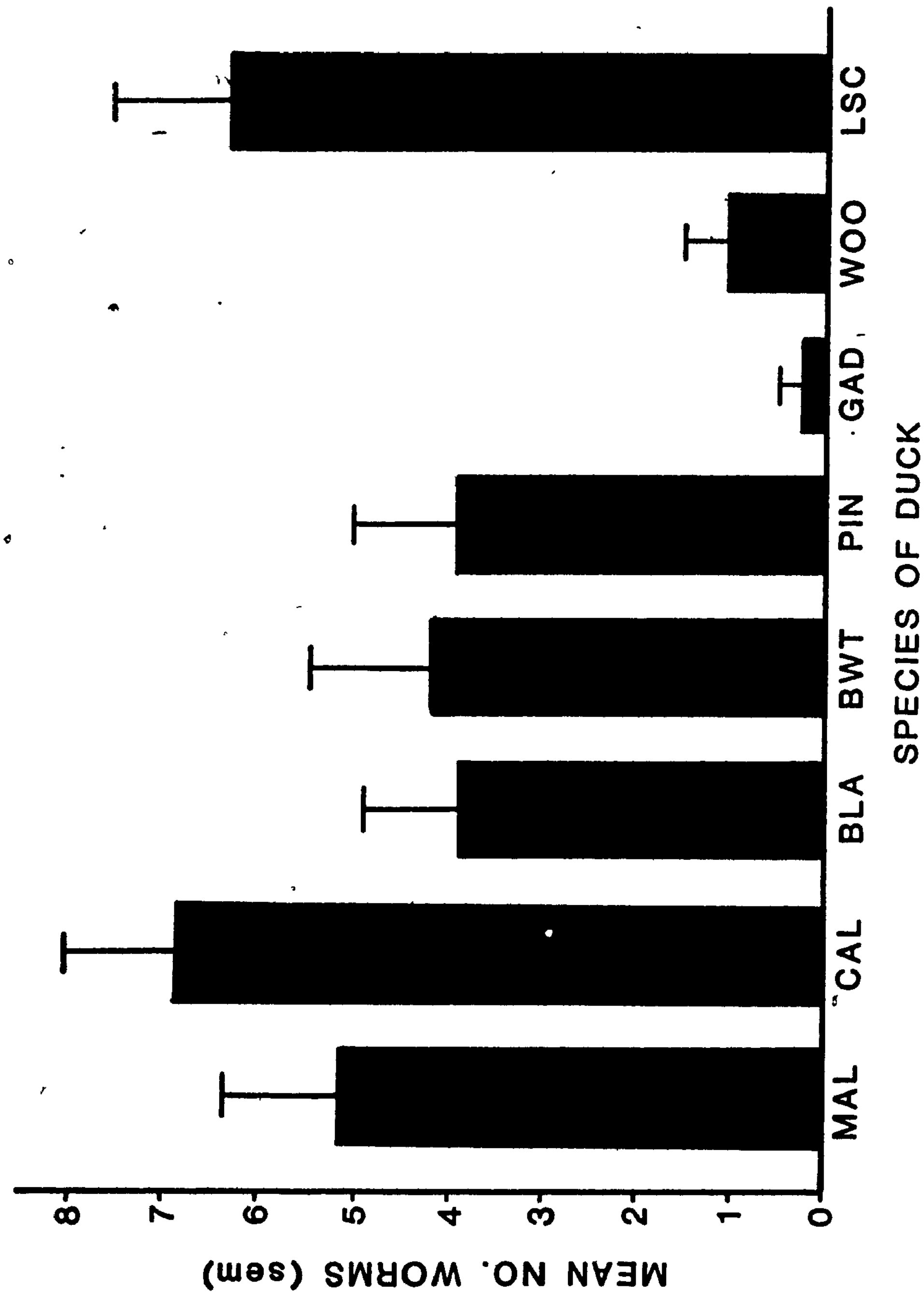

MEAN NO. WORMS (sem)
0
2
4
6
8
10
12
dklg
juv
adult
AGE OF MALLARD

FIGURE 3.

Effect of duck species on the recovery of *Cyathocotyle bushiensis* on Day 7 p.i. All ducks were infected with 25 metacercariae. MAL=mallard (n=20), CAL=call duck (domestic mallard) (20), BLA=black duck (20), BWT=blue-winged teal (15), PIN=pintail (20), GAD=gadwall (4), WOO=wood duck (18), and LSC=lesser scaup (10). Data for gadwalls are presented here but were not included in the analysis due to the small sample size.


MEAN NO. WORMS (sem)
0
1
2
3
4
5
6
7
8
MAL
CAL
BLA
BWT
PIN
GAD
WOO
LSC
SPECIES OF DUCK

no significant differences among the other duck species (H=9.2213, df=5, P>0.05).

The pathology present was a function of worm burden (Appendix 1). Therefore, each cecum was treated as an individual sampling unit. Five ducks showed pathology in at least one cecum but no *C. bushiensis* were recovered from either cecum. All five ducks were pintails, and parasite egg production was not measured for pintails so that the infection cannot be confirmed by the detection of parasite eggs in the feces. Pathology measurements from ceca with no worms were not included in subsequent analyses. There were no significant differences among any of the species or age classes examined in terms of the absolute area affected by hemorrhagic spots (H=12.5259, df=6, P>0.05) (Table 1). The development of plaque formations, also measured in terms of absolute area affected, showed considerable and statistically significant (H=42.4590, df=6, P<0.001) differences among species and age classes (Table 1). Mallard ducklings and pintails developed significantly less plaque formation/worm compared to the other duck species (Figure 4). Similarly, there were considerable and statistically significant (H=40.2803, df=6, P<0.001) differences among species for core development (Table 1). Blue-winged teal showed much greater core development, and mallard ducklings and juveniles showed less, than the other duck species (Figure 4).

The previous analyses were based on absolute measures of pathology. To compensate for the different sizes of ceca in the different duck species, the measures of pathology were corrected for the size of the ceca (Table 1). The results were generally similar to those obtained from the absolute measures. There were significant differences among species for the proportional area affected by hemorrhagic spots (H=13.5960, df=6, P<0.05), proportional area affected by plaque formations (H=41.6029, df=6, P<0.001), and proportional core formations (H=48.1280, df=6, P<0.001), but the species grouped as they did in the analyses using absolute measures (Figure 4).

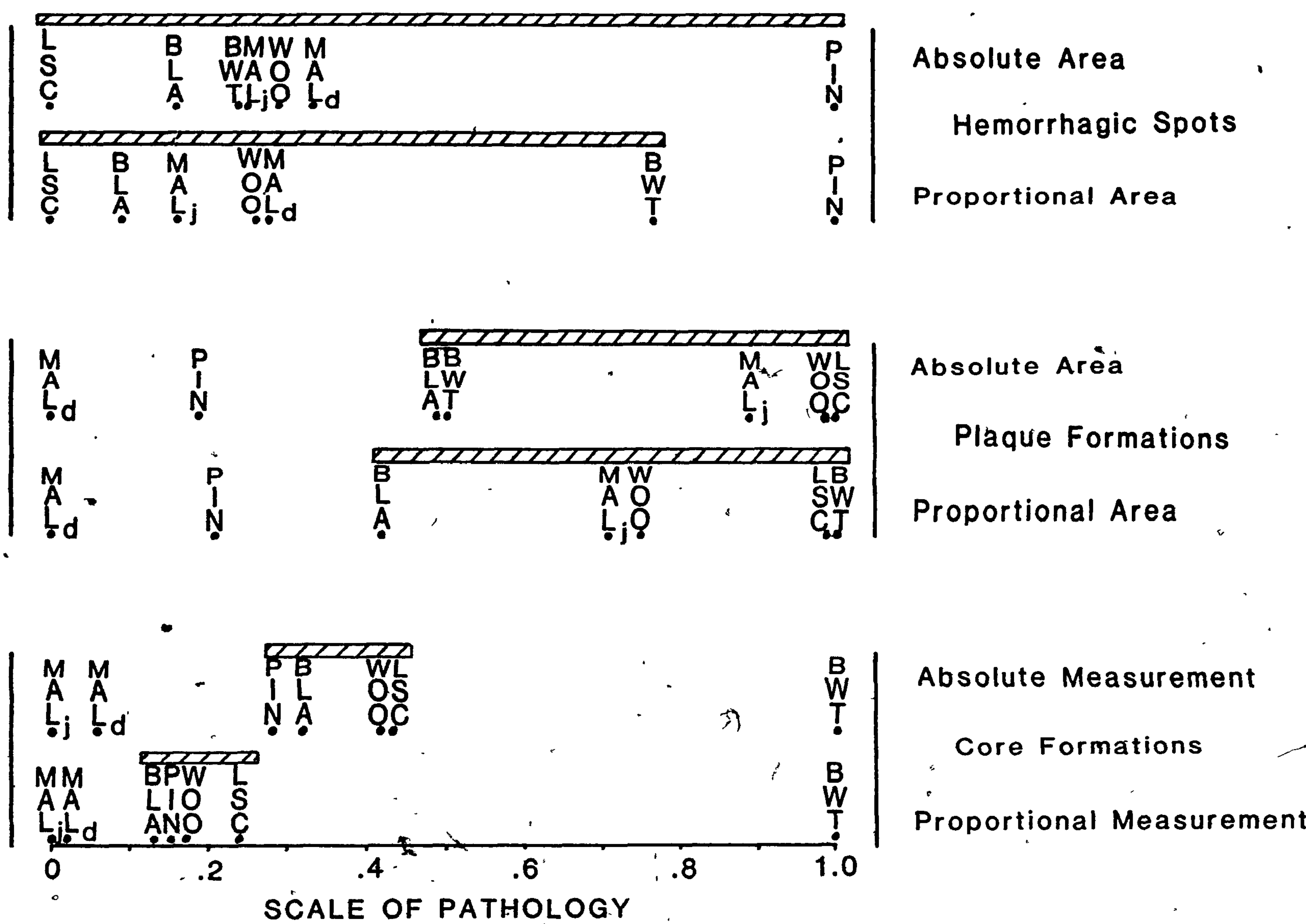
TABLE 1: COMPARISON OF CECAL PATHOLOGY IN DUCKS EXPERIMENTALLY INFECTED WITH *Cyathocotyle bushiensis*.

			Absolute Area[1]			Proportional Area[1]		
Species	Age	n	Hemorrhagic Spots[2]	Plaque Formations[2]	Core Formations[3]	Hemorrhagic Spots[4]	Plaque Formations[4]	Core Formations[5]
Mallard	Duckling	32	0.57 (0.37)	0.86 (0.78)	0.018 (0.052)	0.78 (0.58)	1.09 (1.06)	0.21 (0.58)
Mallard	Juvenile	14	0.51 (0.37)	4.55 (2.87)	0.004 (0.016)	0.66 (0.53)	5.66 (3.54)	0.04 (0.16)
Black Duck	Juvenile	15	0.44 (0.42)	2.91 (2.24)	0.106 (0.171)	0.58 (0.62)	3.79 (3.10)	1.12 (1.77)
Pintail	Juvenile	21	1.07 (1.01)	1.66 (1.34)	0.093 (0.144)	1.59 (1.50)	2.42 (2.06)	1.26 (2.13)
Blue-winged Teal	Juvenile	7	0.50 (0.50)	2.93 (3.59)	0.321 (0.135)	1.33 (1.42)	7.56 (7.43)	8.38 (2.60)
Wood Duck	Juvenile	10	0.54 (0.60)	4.96 (2.64)	0.136 (0.168)	0.77 (1.17)	5.93 (2.82)	1.49 (1.79)
Lesser Scaup	Juvenile	19	0.32 (0.33)	5.02 (4.38)	0.140 (0.134)	0.48 (0.54)	7.53 (6.86)	2.04 (1.98)

1 - mean (standard deviation)
2 - measured as : area affected (# dots)/worm/cecum
3 - measured as : core weight (grams)/worm/cecum
4 - measured as : area affected (%)/worm/cecum
5 - measured as : core weight (grams)/worm/area of cecum (total # dots) X 1000

FIGURE 4.

Comparison of pathology measurements among species and age classes of ducks, for measures of both absolute and proportional area or extent. Scale of Pathology: for each of the six measures, the lowest value was set equal to 0, the highest value set equal to 1.0, and the remaining values were scaled in between. Species under the hatched bars are those not significantly different (P>0.05) after species had been dropped one by one from Kruskal-Wallis analysis. MALd=mallard duckling, MALj=mallard juvenile, BLA=black duck, BWT=blue-winged teal, PIN=pintail, WOO=wood duck, and LSC=lesser scaup.


Absolute Area
Hemorrhagic Spots
Proportional Area
Absolute Area
Plaque Formations
Proportional Area
Absolute Measurement
Core Formations
Proportional Measurement
0
.2
.4
.6
.8
1.0
SCALE OF PATHOLOGY

DISCUSSION

Mallard ducklings harboured significantly more *C. bushiensis* on Day 7 p.i. than did juvenile or adult mallards. This might suggest that a greater proportion of the infective dose of 25 metacercariae excysted and established in the ceca of ducklings than in older birds. Alternatively, initial establishment may have been similar but *C. bushiensis*, once established, may have persisted longer in the ceca of ducklings than in older birds. The life span of *C. bushiensis* has been reported to be from 5 to 10 days (Gibson *et al.*, 1972). In this study, all birds were examined on Day 7 p.i. to allow for the development and subsequent measurement of pathology. However, by Day 7 p.i., some ducks were examined which exhibited the characteristic pathology of infection but no *C. bushiensis* were recovered, suggesting that the worms had already been eliminated.

Field studies have shown that ducklings and juveniles tend to be more heavily infected with many parasites than adult ducks (Cornwell and Cowan, 1963; Buscher, 1965; Buscher, 1966; Crichton and Welch, 1972). Drobney *et al.* (1983) have demonstrated that high levels of parasitism in egg-laying female wood ducks can be correlated with hyperphagia and an increased consumption of invertebrates. Because ducklings feed almost exclusively on invertebrates during their first few weeks of life (Chura, 1961; Sugden, 1973), this increased parasitism may similarly result from increased exposure to the infective stages of many parasites. The present experimental results suggest that, in addition to increased exposure to infective stages, the increased levels of parasitism in young wild ducks may result from a greater innate susceptibility to infection or a decreased ability to resolve an infection once established.

Parasite surveys of wild waterfowl have repeatedly shown that duck species differ in their infection levels for many different parasites (Buscher, 1965; Beverly-Burton, 1972; Crichton and Welch, 1972; Mahoney and Threlfall, 1978; McLaughlin and Burt, 1979; Scott *et al.*, 1979). These differences may be the result of differences in worm establishment and survival among duck species or different levels of exposure to the infective stages based on interspecific differences in feeding ecology. Spieker (1978, in Wobeser, 1981) has shown that duck species are not all equally susceptible to duck virus enteritis. Crichton and Welch (1972) reported that mallards were more parasitized than pintails and speculated that, because mallard and pintail diets are similar, these differences resulted from a greater susceptibility of mallards to parasitic infection. In contrast, Scott *et al.* (1979) found that 4 species of ducks (mallard, blue-winged teal, gadwalls and canvasbacks *Aythya valisineria*) were all equally susceptible to experimental infection with *Typhlocoelum cucumerinum*, a tracheal digenean, thus supporting the hypothesis that most waterfowl trematodes are not host-specific for duck species (Wobeser, 1981). The results of these experimental infections also tend to support that hypothesis; with the exception of wood ducks, all species of ducks examined were equally susceptible to experimental infection with *C. bushiensis*. Although generally considered as a dabbling duck, the wood duck is the only North American member of the Tribe Cairinini, perching ducks (Bellrose, 1976).

Examination of hunter-shot ducks revealed that duck species differed in their *C. bushiensis* infection levels (Hoeve, Chapter 1). The present experimental infections indicate that there are no differences in susceptibility to *C. bushiensis* infection among the dabbling (*Anas* spp.) and diving (*Aythya* spp.) ducks examined. The varying infection levels in wild ducks therefore probably result from varying exposure to the metacercariae.

Cyathocotyle bushiensis has been implicated as a cause of late-summer mortalities of ducks in southern Québec (Gibson *et al.*, 1972; Hoeve, Chapter 1). Duck species present in southern Québec differ in their susceptibility to this parasite-induced mortality (Hoeve, Chapter 1) and can be ranked according to their proportional representation in "dead duck" and "hunter-shot duck" samples (Table 2). The second intermediate hosts for *C.*

TABLE 2: DUCK SPECIES RANKED FOR SUSCEPTIBILITY TO PARASITE-INDUCED MORTALITY AND % SNAILS IN FALL DIET.

Duck Species	Susceptibility to Mortality: Proportion of Sample[2] "Dead Ducks"	Susceptibility to Mortality: Proportion of Sample[2] Hunted	Susceptibility to Mortality: Susceptibility Index[3]	Susceptibility to Mortality: Rank	Feeding Ecology[1]: # Ducks Examined	Feeding Ecology[1]: % Snails in Diet	Feeding Ecology[1]: Rank
Wood Duck	0.000	0.121	0.0	1	38	0.0	1.5
Gadwall	0.016	0.063	0.3	2	47	0.0	1.5
Pintail	0.016	0.022	0.7	4	148	0.3	3
Green-winged Teal	0.049	0.058	0.8	5	318	0.5	4
Mallard	0.180	0.358	0.5	3	1467	0.6	5
Black Duck	0.230	0.184	1.3	6	9	0.1	6[4]
Blue-winged Teal	0.492	0.078	6.3	7	19	4.8	7

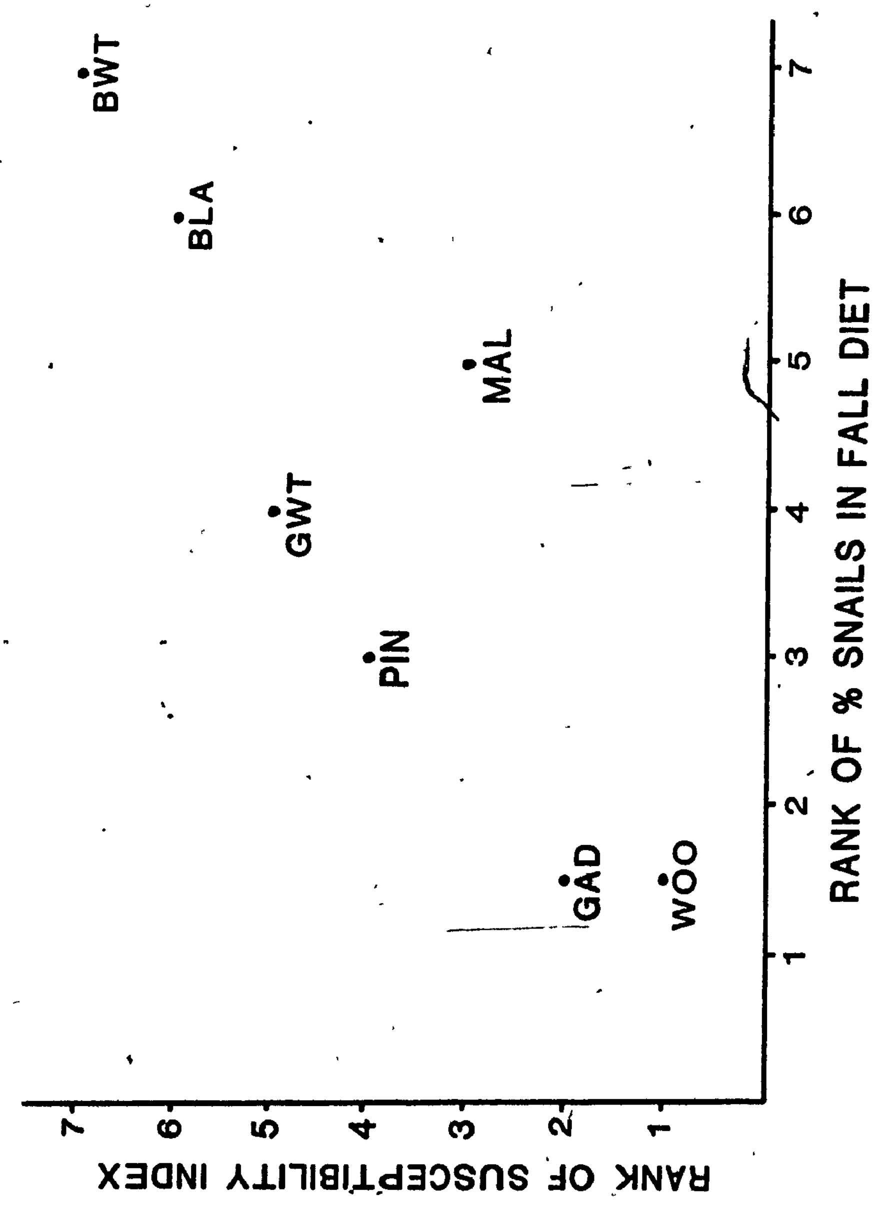
1 - from Korschgen (1955).
2 - from Hoeve (Chapter 1)
3 - Susceptibility Index = proportion of "dead duck" sample / proportion of hunted sample
4 - adjusted rank, see text

bushiensis are freshwater snails (Khan, 1962) and in southern Québec, *Bithynia tentaculata* is the only species of snail from which metacercariae have been recovered (Gibson *et al.*, 1972; Ménard, in preparation). If the differential mortality observed among duck species is a function of feeding ecology, then infection and subsequent mortality should be correlated with the amount of snails in the diets of different duck species. Korschgen (1955) examined the fall food habits of waterfowl in Missouri and included in his data the percentage of snails in the diet. Because gizzard contents were examined, the actual values for percent snails in the diet may be underestimates (Swanson and Bartonek, 1970) but they are still useful for comparisons among species. Using Korschgen's results, duck species have been ranked according to the amount of snails in their diets (Table 2), with one correction. Korschgen examined only 9 black ducks and recorded a low value (0.1%) for percent snails in the diet. Yet black ducks are generally acknowledged to feed more extensively on aquatic invertebrates, and particularly molluscs, than the closely-related mallards (Martin *et al.*, 1951; Bellrose, 1976), so that the rank for black ducks has been adjusted higher than the rank for mallards (Table 2). Spearman's rank correlation analysis (Zar, 1974) yielded a significant positive relationship ($r_s = 0.884$, $P < 0.05$) between the amount of snails in the diet and a duck species' susceptibility to parasite-induced mortality (Figure 5).

This analysis has assumed that *C. bushiensis* is responsible for the annual duck mortalities. However, there is strong evidence that another digenean, *Sphaeridiotrema globulus* is involved in the mortalities (Hoeve, Chapter 1). *S. globulus* also uses *B. tentaculata*, as well as other species of freshwater snails, as second intermediate hosts (Huffman and Fried, 1983). If trematodes generally are not host-specific for duck species (Wobeser, 1981), a hypothesis that these experimental infections support, it is probable that duck species have no differences in susceptibility to infection with *S. globulus*. Then, because ducks acquire both parasites by eating snails, the preceding analysis of feeding ecology would apply equally

FIGURE 5.

Spearman's rank correlation analysis of percent snails in fall diet plotted against species susceptibility to parasite-induced mortality. Data for percent snails in diet were taken from Korschgen (1955). MAL=mallard, BLA=black duck, BWT=blue-winged teal, GWT=green-winged teal, PIN=pintail, GAD=gadwall, and WOO=wood duck.


RANK OF SUSCEPTIBILITY INDEX
RANK OF % SNAILS IN FALL DIET
1
2
3
4
5
6
7
BWT
BLA
MAL
GWT
PIN
GAD
WOO

well to *S. globulus* infections, or to the concurrent infections with both *C. bushiensis* and *S. globulus* which were found in almost all "dead ducks" examined (Hoeve, Chapter 1).

Generally, the results of the pathology measurements were similar whether the measurements were based on absolute area affected or on proportional area corrected for ceca size. Hemorrhagic spots are created at the sites of attachment of the worms, where the epithelial cells lining the cecum are extracorporeally digested (Erasmus and Ohman, 1963). The worms move from one spot to another so that a "trail" of hemorrhagic spots occurs on the cecal wall. The absolute area affected by hemorrhagic spots was the same for all ages and species of ducks examined but the relative area affected was significantly higher in pintails. The general similarity of this measurement among duck ages and species suggests that the worms behave similarly in the different species of hosts. The area of hemorrhagic spots is a measure of the pathology produced directly by the parasite.

In contrast, plaque and core formations result from host responses and are therefore host-induced pathologies. The fibrin secretion which creates plaque formations seems to be a delayed response, occurring at the sites of previous hemorrhagic spots. In more heavily infected birds, the fibrin secretions are occasionally extreme enough to produce a core in the lumen of the cecum, sometimes blocking the entire cecum. The measurements of plaque and core formations did show significant differences with age and among duck species. Because plaque and core formations may be measurements of different extremes of essentially the same response, it might be artificial to separate them. For example, juvenile mallards showed little core formation but fairly high plaque formations. Therefore, looking at the total host-induced pathology (plaque plus core formations), two points are clear. First, ducklings have the least development of host-induced pathology; perhaps this is involved in some way with the suggestion made earlier that ducklings may have a decreased ability to resolve infections. Second, blue-winged teal have by far the greatest development of host-induced pathology, resulting mainly from extensive core formations. It is interesting that blue-winged teal is also the species that, based on field data, is most susceptible to the annual mortality in southern Québec (Hoeve, Chapter 1).

It should be noted that these measurements of pathology were highly variable, producing an inconsistent gradient of responses in different duck species, so that it is difficult to know what effect, if any, the cecal pathology produced by *C. bushiensis* infections has in the observed duck die-offs. This uncertainty is fostered by two observations. The first is that none of these ducks died or even appeared ill due to the experimental *C. bushiensis* infections (pers. obser.). Second, the mortality seems to be more closely associated with *S. globulus* worm burdens than with *C. bushiensis* worm burdens (Hoeve, Chapter 1).

Although there seems to be little correlation between the cecal pathology caused by *C. bushiensis* and the annual duck die-offs, these experimental infections do provide valuable information concerning the epizootiology of the die-offs. Almost all duck species examined were equally susceptible to experimental infection. Therefore, the varying infection levels and the differing effects of the mortality among the duck species probably results from different levels of exposure to the metacercariae, based on the amount of snails in the ducks' diets.

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CONNECTING STATEMENT

Chapter 1 showed that a recurrent late-summer mortality of dabbling ducks was probably parasite-induced, and that all duck species were not equally affected by the infection and mortality. In Chapter 2, it was shown that almost all species of ducks examined were equally susceptible to experimental infection with *Cyathocotyle bushiensis*, and it was suggested that differences in feeding ecology were responsible for the observed differences among duck species. Therefore, duck species eating more aquatic snails were likely to become infected and were more likely to die from the infection.

It was also shown in Chapter 1 that the mortality was highly seasonal, as two thirds of all "dead ducks" recovered were collected during the last two weeks of August. One possible explanation for the regular occurrence of the mortality during late-summer was that seasonal changes in the prevalence or abundance of metacercariae in aquatic snails could enhance transmission during late-summer. In Chapter 3, sentinel ducks were used to determine if seasonal changes in the availability of metacercariae to ducks were responsible for the timing of the mortalities.

CHAPTER 3

SEASONALITY OF PARASITE-INDUCED DUCK MORTALITY.*

BY

HOEVE, J. AND M.E. SCOTT

* for submission to the Journal of Wildlife Diseases.

ABSTRACT

Sentinel ducks were used to determine if seasonal changes in the availability of *Sphaeridiotrema globulus* (Rudolphi, 1814) and or *Cyathocotyle bushiensis* Khan, 1962 metacercariae could explain the regular occurrence of parasite-induced duck mortalities during late-summer. Acquisition of *C. bushiensis* was not significantly different for each month from May to September; acquisition of *S. globulus* was low in May and June, and higher but not significantly different from July to September. This suggests that seasonal changes in availability of *C. bushiensis* metacercariae are not responsible for the regularity of the mortalities. Data on *S. globulus* are less conclusive, and further studies are needed to determine the role of seasonal availability of these metacercariae in the late-summer duck mortality. Preliminary experiments indicate that small initial infections with *C bushiensis* produce a degree of acquired resistance to re-infection. It is suggested that the occurrence of the mortalities during late-summer may result either from an annual, pre-migration arrival of large numbers of ducks to feed on the productive but highly infective marshes of the St. Lawrence River and its tributaries and/or the seasonal occurrence of *S. globulus* metacercariae.

INTRODUCTION

In 1972, Gibson *et al.* reported that late-summer mortalities of ducks on the St. Lawrence River in southern Québec were caused by the digenean *Cyathocotyle bushiensis* Khan, 1962. Similar, late-summer mortalities have continued to occur in southern Québec since that time (R. Parent, Waterfowl Biologist, pers. comm.; Demers, 1985). Hoeve (Chapter 1) has shown that the mortality was concentrated during the last two weeks of August during the summers 1983 to 1985. It was also shown that, although *C. bushiensis* was still associated with the duck mortalities, another digenean *Sphaeridiotrema globulus* (Rudolphi, 1814) was probably more important as the cause of the mortalities during these years (Hoeve, Chapter 1).

The purpose of this study was to examine factors which might be responsible for the mortality occurring so regularly during late-summer. Sentinel ducks were used to monitor the seasonal acquisition of parasites in 1985, to test whether changes in the availability of metacercariae to ducks could explain the mortality. The Rivière du Sud, Québec, was chosen as the site for the sentinel duck experiment for 3 reasons: first, "dead ducks" (Hoeve, Chapter 1) had been collected there during the two previous summers; second, the population of *Bithynia tentaculata* (Gastropoda: Prosbranchia) was known to be abundant and had been found to be heavily infected with *C. bushiensis* metacercariae during the previous summer (Ménard, in preparation); and third, a study of the transmission of larval stages of *C. bushiensis* and *S. globulus* using sentinel snails was simultaneously being conducted there (Ménard, in preparation). To complement this field study using sentinel ducks, experimental infections were used to determine if small initial infections with *C. bushiensis* could produce acquired resistance to reinfection, as Macy (1973) has demonstrated for *S. globulus*.

STUDY AREA

The Rivière du Sud has long been recognized as an ecologically unique and valuable area, as recently summarized in an assessment report (CTARS, 1984); most of the following description is taken from this report. The Rivière du Sud (45°6' N; 73°14' W) is located approximately 50 Km southeast of Montréal (Figure 1) in a gently rolling area of the St. Lawrence Lowlands. The surrounding area is productive agricultural land, with most of the acreage devoted to corn production (pers. obser.). Annual spring flooding has maintained a border of riparian forest along both banks of the river, composed mainly of silver maple (*Acer saccharinum*), swamp white oak (*Quercus bicolor*) and black willow (*Salix nigra*).

After spring flooding, the river where the cages were built is approximately 200 metres (m) wide, the current is negligible and the discharge is small, with water depth varying between 1/2 and 1 1/2 m. The site is eutrophic and aquatic vegetation is abundant, including wild celery (*Vallisneria americana*) and wild rice (*Zizania aquatica*). Thus, during most of the summer, the Rivière du Sud more closely resembles a large marsh than a river. This region supports breeding populations of blue-winged teal (*Anas discors*), mallards (*Anas platyrhynchos*), black ducks (*Anas rubripes*) and wood ducks (*Aix sponsa*). The cages were built in a portion of the river (Figure 2) intensively used by these species for feeding during late-summer. Recognized as being among the best waterfowl habitat in southern Québec, it has been suggested as a site for protection and management (Canards Illimités Canada, 1981).

MATERIALS AND METHODS

Two cages were built, each approximately 3 X 3 m, using standard chicken wire mesh supported on 5 cm X 5 cm X 2.4 m (2" X 2" X 8') wooden stakes. The cage sites were selected where late-summer water depth was expected to be about 1/2 m; when the cages were built in early May, 1985, water depth was slightly less than 1 m. Water levels dropped more than anticipated, and Cage #1 dried up between the July and August sampling periods. Therefore, Cage #1 was moved approximately 20 m toward midstream for the last two months.

FIGURE 1.

Map of southwestern Québec, showing the location of the Rivière du Sud study area.

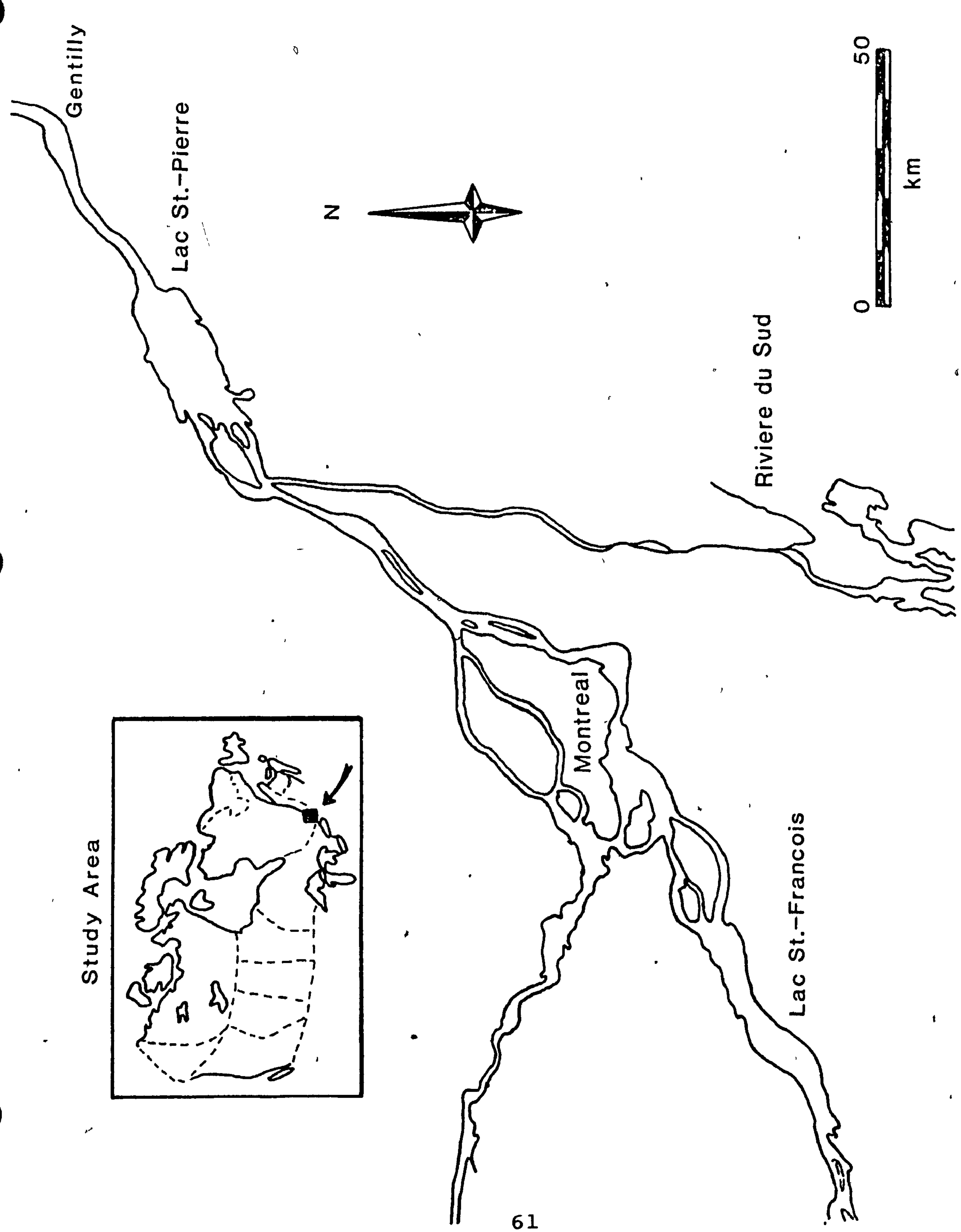
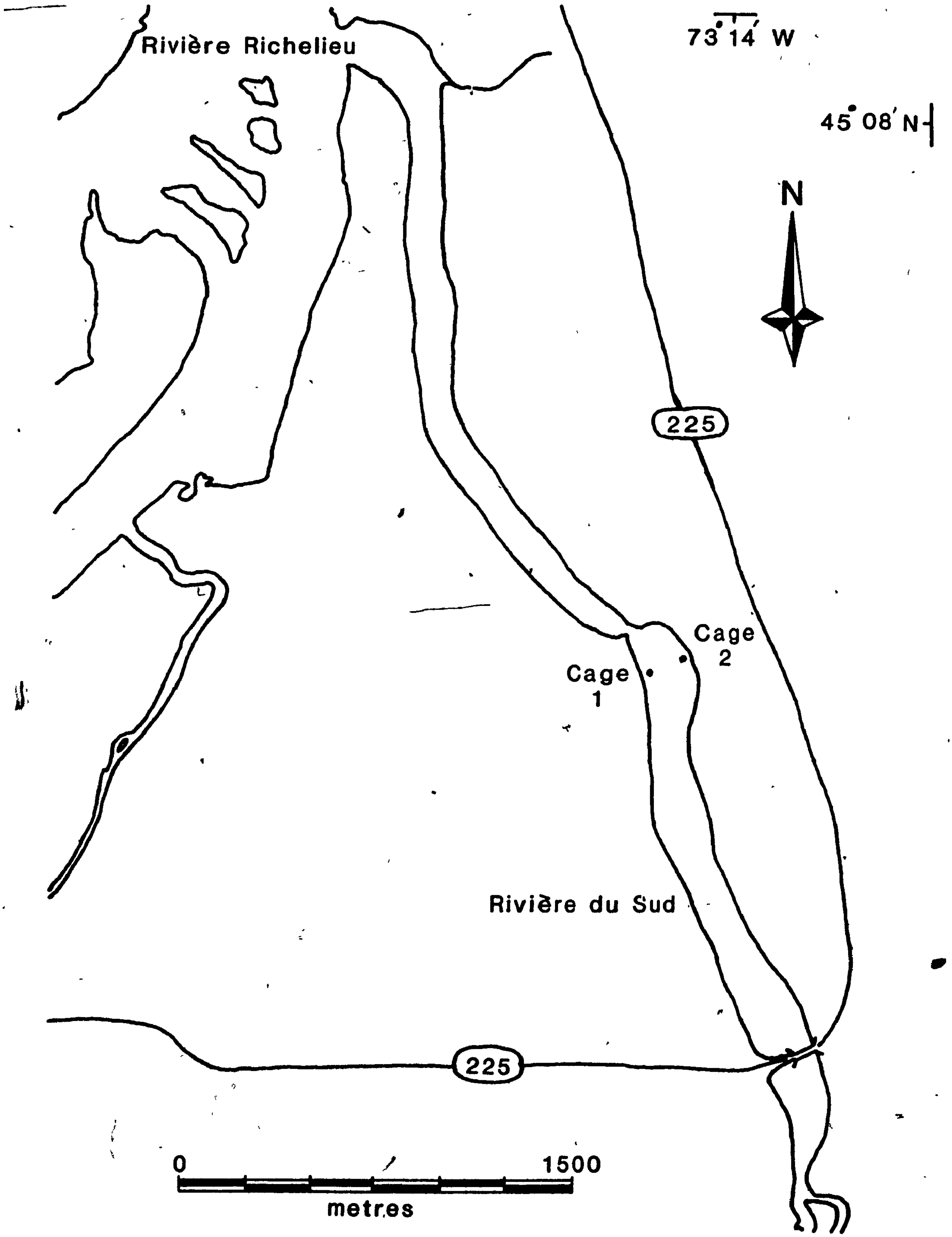

Gentilly
Lac St.-Pierre
N
0
50
km
Riviere du Sud
Montreal
Lac St.-Francois
Study Area

FIGURE 2.

Map of the Rivière du Sud, showing the locations of the cages for the sentinel ducks.


73°14' W
45°08' N
N
Rivière Richelieu
225
Cage 2
Cage 1
Rivière du Sud
225
0
1500
metres

Blue-winged teal was the species chosen for use as sentinel ducks because they are known to be susceptible to infection and mortality (Hoeve, Chapter 1) and, among dabbling ducks, they consume the most aquatic snails (Korschgen, 1955). Adult ducks, over-wintered in the laboratory, were used in May, June and July; juvenile ducks were used in August and September. Because susceptibility to infection does not differ significantly between juvenile and adult ducks (Hoeve, Chapter 2) and assuming that feeding behavior does not change, measurement of parasite acquisition should not be affected by switching from adult to juvenile ducks. All ducks were obtained from the suppliers as ducklings and were free of helminth infections.

Three, wing-clipped ducks were placed together in each of the two cages for a period of 24 hours once during the middle of each month from May through September. Ducks were placed in the cages at midday and were removed at midday the following day, thereby allowing uninterrupted feeding during the peak feeding periods in the evening and, to a lesser extent, the early morning (Swanson and Sargeant, 1972; Stoddart, 1985). After removal from the cages, ducks were returned to the laboratory where water and commercial, non-medicated 18% poultry laying mash (Coopérative du Québec, Ste.-Rosalie, Québec) were supplied *ad libitum*. Ducks were killed after 5 to 7 days; intestinal tracts were examined for helminths as described previously (Hoeve, Chapter 2) except that the entire length of the small intestine was examined.

In August and September, samples of *B. tentaculata* were collected from in and around the cages. The snails were crushed individually and the prevalence and abundance of *C. bushiensis* and *S. globulus* metacercariae were recorded. The metacercariae were distinguished based on size and general appearance. Cysts of *S. globulus* were smaller, averaging 0.180 mm (Macy and Ford, 1964) whereas *C. bushiensis* metacercariae averaged 0.239 mm (Khan, 1962). In addition, *C. bushiensis* metacercariae were spherical, possessed a thick, transparent cyst wall and black pigmentation within the cyst. *S. globulus* metacercariae were somewhat flattened, possessed no thick cyst wall and contained brown pigment. Identification was confirmed by collecting mature parasites after experimental infections.

Lab-reared Call ducks (domestic mallards *Anas platyrhynchos*) were used for the experimental infections and were divided into two groups. Five ducks were infected on Day 0 with 25 *C. bushiensis* metacercariae as described in Hoeve (Chapter 2). To estimate worm establishment, duck feces were collected for 24 hours on Day 7 post infection and washed through a series of sieves until the parasite eggs were trapped on a 325 mesh/inch sieve. All feces and eggs from this sieve were suspended in 400 ml of water and the eggs present in 10 aliquots were counted using a McMaster Egg Counting Chamber. The mean value was adjusted to give egg production / 24 hours. On Day 15, when worms from the initial infection should have been eliminated (Gibson *et al.*, 1972, Scott, unpubl. data), the 5 ducks were re-infected with 25 metacercariae. In addition, three ducks were infected as controls for the challenge infection. Seven days later, all ducks were killed and examined as described previously (Hoeve, Chapter 2).

Kruskal-Wallis tests were used to compare worm burdens. Level of significance was set at 5%.

RESULTS

The sentinel ducks acquired both *C. bushiensis* and *S. globulus* infections (Table 1) during the 24 hour exposure period. In June, 1 duck escaped through a hole in the mesh and wasn't recaptured; 2 other ducks were missing from the cages when they were to be removed on the second day. Three ducks died after 5 to 7 days in the laboratory, presumably from the infections. In addition to *C. bushiensis* and *S. globulus*, 1 immature *Zygocotyle lunata* was recovered from 1 duck in August and small numbers (maximum = 6) of immature *Echinostoma revolutum* were recovered from several ducks in August and September.

Even though few *C. bushiensis* were acquired in May and no ducks became infected in June, there was no significant difference in the monthly

TABLE 1: SEASONAL ACQUISITION OF *Cyathocotyle bushiensis* AND *Sphaeridiotrema globulus* BY SENTINEL DUCKS.

	Cage # 1						Cage # 2							
	Duck # 1		Duck # 2		Duck # 3		Duck # 4		Duck # 5		Duck # 6		Mean	
Month	Cyath.	Sphaer.	Cyath.	Sphaer.	Cyath.	Sphaer.	Cyath.	Sphaer.	Cyath.	Sphaer.	Cyath.	Sphaer.	Cyath.	Sphaer.
May	1	0	0	0	3	8	0	0	0	0	0	0	0.7	1.3
June	0	2	0	0	0	3	0	10	-	-	-	-	0.0	3.8
July	14	2117*	0	222	4	971	0	4	0	32	-	-	3.6	669.2
August	13	2757*	1	1078	3	1806	2	1694	0	530	0	135	3.2	1333.3
September	7	1161*	4	843	2	277	1	828	1	1040	0	879	2.5	838.0

* - duck died in laboratory

acquisition of *C. bushiensis* (H=6.4546, df=4, P>0.05). In contrast, acquisition of *S. globulus* was significantly higher in July, August and September than in May and June (H=18.9346, df=4, P<0.001).

From the abundances of metacercariae in *B. tentaculata*, the mean infection levels of *C. bushiensis* could have been acquired by the ducks in August and September by eating between 13 and 62 *B. tentaculata* (Table 2). In contrast, the ducks would have to have eaten between 580 and 1483 *B. tentaculata* to acquire the reported *S. globulus* burdens (Table 2).

Eggs of *C. bushiensis* were detected in the feces of all challenge ducks 7 days post infection. In Call ducks, *C. bushiensis* produce an average of 1595.4 eggs/worm/day (n=19, s.d.=940.0) on Day 7 p.i. with no evidence of density dependence at the worm burdens used (r=-75.33, t_s=1.9414, d.f.=17, P>0.05). Therefore, Day 7 egg production in the challenged ducks was used to estimate the number of worms present from the initial infection (Table 3). Worm burdens in control ducks on Day 22 were not significantly different from the estimated worm burdens in the challenge ducks on Day 7 (H=2.7213, df=1, P>0.05). On Day 22, no worms were found in any of the challenged ducks (Table 3). Therefore, recovery from the challenge infection was significantly lower than from control ducks or the primary infection (H=9.0962, df=1, P<0.01).

DISCUSSION

Sentinel ducks have been used in previous studies, but this has generally involved releasing domestic ducks onto large but restricted water bodies for an entire season to determine which parasite species were acquired (Shaw and Kocan, 1980; Gvozdev, 1985). In this study, ducks were placed in small restricted areas for short periods of time specifically to determine whether seasonal changes in the availability of *S. globulus* and *C. bushiensis* metacercariae to ducks could be responsible for the timing of the late-summer mortality. For both parasite species, acquisition was not significantly different in the months of July, August and September,

TABLE 2: PREVALENCE AND ABUNDANCE OF METACERCARIAE IN <u>Bithynia tentaculata</u> AND THE NUMBER OF SNAILS REQUIRED TO PRODUCE THE OBSERVED INFECTION IN SENTINEL DUCKS.

			Cyathocotyle bushiensis				Sphaeridiotrema globulus			
Month	Cage	#Snails	Prev.[1]	Abun.[2]	Mean # Worms/Duck	Requ'd # Snails	Prev.	Abun.	Mean # Worms/Duck	Requ'd # Snails
Aug.	1	100	10	0.13	5.66	43.5	39	2.47	1880	761
	2	100	3	0.03	0.67	22.3	26	0.53	786	1483
Sept.	1	100	5	0.07	4.33	61.9	40	1.31	760	580
	2	43	4.7	0.05	0.67	13.4	0	0.00	916	-

1 - per cent snails infected
2 - total # metacercariae / total # snails

TABLE 3: ESTABLISHMENT OF *Cyathocotyle bushiensis* DURING PRIMARY AND CHALLENGE INFECTIONS.

			No. Worms	
Group	No.	Day 7 Egg Production	Day 7[1]	Day 22
Challenged	1	19476	12	0
	2	1868	1	0
	3	5336	3	0
	4	4536	3	0
	5	7204	5	0
Control	1	-	-	4
	2	-	-	17
	3	-	-	14

1 - estimated from parasite egg production

suggesting that availability of metacercariae in the snail populations is not the factor determining the late-summer occurrence of the duck mortalities. Support for this observation is provided by Ménard (in preparation), who reported that the abundance of *C bushiensis* metacercariae in *B. tentaculata* populations is actually lowest during late-summer due to the recruitment of uninfected snails born during the summer However, it was found that the rate of infection of sentinel snails with *S. globulus* metacercariae peaked in August (Ménard, in preparation). Examination of Table 1 reveals that the mean number of *S. globulus* acquired by sentinel snails in August was twice as high as in July and 1.6 times as high as in September. Because of the small sample size and the high variability, these values are not statistically different. However, if *S. globulus* is the parasite more directly responsible for the recurrent duck mortality, seasonal availability of metacercariae may contribute to the seasonal mortality. This possibility requires further investigation.

Three of the sentinel ducks died after 5 to 7 days in the laboratory. Because they were three of the most heavily infected ducks and no other causes of mortality were observed, it is probable that they died as a result of the parasite infections. The deaths occurred rapidly; all three ducks were found dead in the cages in the morning but none had appeared stressed or moribund the preceding evening. That these three sentinel ducks, restricted to 3 X 3 m cage, were able to acquire lethal parasite infections in 24 hours demonstrates how quickly wild ducks, free to forage over large areas, could also acquire lethal infections. The deaths of these sentinel ducks also lends support to Hoeve (Chapter 1), who concluded that *S. globulus* and *C. bushiensis* were probably responsible for mortalities of wild ducks, based on comparisons of infection levels in ducks found dead and in hunter-shot ducks.

From the abundance of *C. bushiensis* metacercariae in *B. tentaculata*, it is clear that the infection levels recorded in the sentinel ducks could have been acquired by eating 100 snails or less. For *S. globulus*, however, some of the sentinel ducks must have eaten several hundreds, or thousands, of *B. tentaculata* to acquire the worm burdens recorded. There are at least 2 possible explanations for this discrepancy. First, while *C bushiensis* seems to be restricted to *B tentaculata* as second intermediate host (Gibson *et al.*, 1972; Ménard, in preparation), *S. globulus* is capable of encysting in different snail species (Huffman and Fried, 1983) so that some of the *S. globulus* could have been acquired by eating snails other than *B. tentaculata*; however, *B. tentaculata* is the most abundant snail in this area of the Rivière du Sud (pers. obser.) and it is believed that this explanation would only account for a portion of the discrepancy An alternative explanation is that these samples of *B tentaculata* do not accurately represent the abundance of *S globulus* metacercariae in the snail populations. While crushing *B tentaculata* from the Riviere du Sud to collect *C. bushiensis* metacercariae, *S. globulus* metacercariae were also frequently observed and, although not quantified, the abundance of *S globulus* metacercariae seemed much greater than the values recorded here (pers obser) Therefore, the abundances of *S. globulus* metacercariae recorded here are probably underestimates. Certainly, consuming up to 100 *B. tentaculata*, as suggested by the *C. bushiensis* data, does not seem to be unrealistic for blue-winged teal, whereas consuming more than 1000 *B. tentaculata* in one day seems unlikely It is difficult to explain why random sampling of snails would appear to accurately represent the abundance of *C bushiensis* but not that of *S. globulus*.

For the experimental infections, all of the challenge ducks became infected from the initial inoculum, as proven by the detection of *C. bushiensis* eggs in the duck feces. In the challenge ducks, no worms survived from the second infection on Day 15 until necropsy on Day 22, suggesting that these ducks had developed some degree of acquired resistance. These preliminary results agree with those of Macy (1973), who demonstrated acquired resistance to reinfection for *S. globulus*. Some degree of acquired resistance has also been reported in ducks infected with

Trichobilharzia ocellata, as measured by parasite egg production (Rau *et al.*, 1975).

The sentinel ducks have shown that transmission of *S. globulus* and *C. bushiensis* occurs at low levels early in the summer, during May and June. Resident breeding ducks on the St. Lawrence River marshes and the Rivière du Sud may acquire sublethal infections early in the summer and thereby develop some degree of resistance to larger, potentially lethal infections later in the summer. Therefore, it is probably not resident ducks which are most affected by the mortality.

Sphaeridiotrema globulus has been reported once from wood ducks; two of 34 ducks collected in New England were infected (Thul *et al.*, 1985). Other surveys of waterfowl parasites in Ontario and eastern Canada (Turner and Threlfall, 1975; Mahoney and Threlfall, 1978; McLaughlin and Burt, 1979) have not reported *S. globulus* or *C. bushiensis*, and no *C. bushiensis* were reported from the wood ducks examined by Thul *et al.* (1985). The only region where both parasites are commonly found seems to be the St. Lawrence River system in southern Québec (Hoeve, Chapter 1).

Patterson (1976) examined factors regulating duck populations and found that, while behavioral spacing mechanisms acted to disperse breeding ducks early in the season, these mechanisms act less and less strongly throughout the summer, and nutrition becomes a more and more important factor. Therefore, ducks gather to feed in large flocks on the most productive waters during late-summer. In late-summer, the productive marshes of the St. Lawrence River and its tributaries attract large numbers of ducks from surrounding areas, (L.M. Soyez, pers. comm.). Because the region of common occurrence of *S. globulus* and *C. bushiensis* seems to be limited to the St. Lawrence River system, many of these ducks may be "naive", never having been exposed to either parasite before. As the sentinel ducks have shown, these "naive" ducks, arriving to feed on the productive but highly infective marshes, can acquire lethal infections in as little as 24 hours. Therefore, the timing of the mortality during late-summer seems to result from seasonal changes in the factors regulating duck distributions, and/or from the pattern of seasonal availability of *S globulus* metacercariae.

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CONCLUSION

A recurrent, late-summer mortality of dabbling ducks in southern Québec was examined under the hypothesis that it was parasite-induced. In Chapter 1, comparison of parasite infection levels between ducks found dead and hunter-shot ducks revealed that two digeneans, *Sphaeridiotrema globulus* and *Cyathocotyle bushiensis*, were significantly more prevalent in the ducks found dead. Comparison of the intensity of infection of these two parasites showed that *S. globulus* infections were almost always significantly larger in ducks found dead; although *C. bushiensis* infections tended to be larger in ducks found dead, the differences were usually not statistically significant. It was concluded that heavy infections with these two parasites were the major cause of late-summer duck mortalities, but that *S. globulus* was the more important pathogen.

In Chapter 2, experimental infections with *C. bushiensis* were used to determine if differences in innate susceptibility to infection could explain observed differences among duck species in terms of prevalence and intensity of infection, and in terms of disproportionate species representation in samples of dead ducks. Almost all species of ducks examined were equally susceptible to infection and it was suggested that interspecific differences in feeding ecology caused the observed differences. Therefore, duck species eating more aquatic snails were most frequently and most heavily infected, and most likely to die from the infection.

In Chapter 3, it was shown that acquisition of both *S globulus* and *C. bushiensis* by sentinel ducks was similar from July through September, indicating that seasonal changes in the availability of metacercariae to ducks was probably not responsible for the regular occurrence of the mortality during late-summer (end of August). It was suggested that an annual pre-migration arrival of large numbers of possibly "naive" ducks from surrounding areas to feed on the infective marshes of the St. Lawrence River may be the cause of the seasonality of the mortality.

APPENDIX 1:

RESULTS FROM REGRESSION ANALYSES, SHOWING THE GENERAL DEPENDENCE OF AMOUNT OF CECAL PATHOLOGY ON THE NUMBER OF *C. bushiensis* PRESENT IN CECUM.

RESULTS FROM REGRESSION ANALYSES, SHOWING THE GENERAL DEPENDENCE OF AMOUNT OF CECAL PATHOLOGY ON THE NUMBER OF *C. bushiensis* PRESENT IN CECUM.

			Hemorrhagic Spots		Plaque Formations		Core Formations	
Species	Age	n	t	P[1]	t	P	t	P
Mallard	dklg.	40	5.081	***	5.056	***	1.529	N.S.
Mallard	juv.	20	4.599	***	8.103	***	1.034	N.S.
B.W. Teal	juv.	14	2.305	*	2.116	N.S.	5.686	***
Pintail	juv.	40	3.866	***	2.095	*	3.553	**
Black Duck	juv.	18	1.985	N.S.	4.295	***	3.310	**
Wood Duck	juv.	34	7.316	***	13.993	***	8.597	***
Lesser Scaup	juv.	20	0.903	N.S.	3.920	**	0.523	N.S.

1 : N.S. - $P>0.05$; * - $P<0.05$; ** - $P<0.01$; *** - $P<0.001$