

## COMMUNITY ECOLOGY OF THE HELMINTH PARASITES OF THE BROWN PELICAN

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Research on the dynamics of communities can be very rewarding, for it can reveal the processes that determine the character of the community. However, some kinds of communities are difficult to observe, so their nature and dynamics remain obscure. Communities of parasites living inside other organisms can be studied only by killing the hosts, enabling only a single, momentary view of the community within each. To learn the dynamics of such a community, it is necessary to build a composite view from a series of samples. Ecologists have found numerical diversity analysis to be a powerful tool for understanding obscure communities through indirect data, for diversity focuses attention on particular species, locations, times of year, or biological processes that are influential in community dynamics. An exemplary study (Hair and Holmes 1975) of parasites in the Lesser Scaup (*Aythya affinis*) shows the power of diversity analysis by demonstrating spatial displacement of parasites of the small intestine—apparent solutions to competition for shared resources.

The community studied here is the helminth fauna (Courtney and Forrester 1974) of the Brown Pelican (*Pelecanus occidentalis*). Careful inspection of the organs uncovers a separate example of the community for each bird sampled. By choosing replicate samples in different geographic locations and of different host age, it is possible to examine community structure as a function of region and successional age. This paper describes community succession in pelican helminths, provides evidence of competition among the parasites, and suggests host responses that suppress the parasite community, and shows effects of food intake and zoogeography on the community.

### METHODS

Fifty-three fledged birds were collected from widely scattered localities on the coasts of peninsular Florida. Nine nestlings were obtained from various colonies on the Atlantic coast, and 30 nestlings were taken from Bird Key (Lee County) on the Gulf coast. Fourteen pelicans that had been shot or found dead on Grand Terre, Louisiana, also were examined. The Louisiana pelicans had been transplanted from the Atlantic coast of Florida as nestlings in 1968, 1969, and 1970. Collections were from 1971 through 1973 and provided no control over possible seasonal cycling of parasite populations. For analysis, the birds were separated into age classes and were grouped into three localities—the Atlantic coast of Florida, the Gulf coast of Florida, and Louisiana.

Some birds were examined shortly after death, but most were frozen when received. At necropsy the birds were dissected and the following examined: esophagus, proven-

trculus, duodenum, ileojejenum, ceca, small and large intestine, cloaca, heart, trachea, lungs, liver, gall bladder, kidneys, nasal cavity, orbit, subcutaneous tissues, and body cavity. Procedures for recovering, killing, fixing, and studying helminths were those described by Kinsella and Forrester (1972). Where trematodes were small and numerous, their numbers were determined by mixing them thoroughly with 250 ml of water and counting a 10 ml aliquot.

Two taxonomic problems introduced bias into the subsequent data analysis. We treated all individuals of *Contracaecum* as 1 species complex, but 2 species were present (*C. spiculigerum* and *C. multipapillatum*). The differentiated species occurred about equally in our samples. *Phagicola longus* and *P. sp. cf. minutus* were treated as one species. The unidentified species of *Phagicola* was always accompanied by greater numbers of *P. longus* and was found only 3 times—twice in Florida Atlantic coast nestlings and once in Florida Gulf coast nestlings.

Comparisons were of helminth communities from fledged birds on all 3 coasts and of helminths from birds in an age series (2 week nestlings to adults) on Florida's Gulf and Atlantic coasts. Communities were evaluated by quantifying the parasite load of each bird age class and measuring the diversity of the communities with indices derived from information theory. Indices used here are for species diversity,  $H' = -\sum p_i \log_e p_i$  (Shannon and Weaver 1949), where  $p_i$  is the number of the  $i^{\text{th}}$  species divided by sample size, and equitability,  $E = H'/H_{\text{max}}$  (Sheldon 1969), where  $H_{\text{max}}$  is the natural log of the number of observed species. A component of  $H'$ ,  $H'_{n_1}$ , is the contribution to the diversity value by the most abundant species. That is,  $H'_{n_1} = -p_1 \log_e p_1$ . This value (1) makes it possible to judge the importance of each species in its community and (2) in cases where 1 species is overwhelmingly common, establishes a criterion ( $H'_{n_1} < H'_{n_2}$ ) for attributing an inequitable distribution of relative abundances to a superabundant species. In such cases, the apparent disadvantage of the distorted index value is offset by the signal that some environmental resource is inequitably distributed among species. That indicates that the resource occurs in only a few forms or that the most abundant species is exceptionally well adapted to use the resource, or both.

Sample parameters are given in Table 1. The testing of sample size by calculating diversity with successively pooled sample data, as prescribed by Wilhm (1970a), works in a peculiar fashion with parasite communities. Rather than steadily progressing toward an asymptote, parasite diversity values exhibit great variance. This happens because the few extremely heavy infestations that overwhelmingly reduce diversity are likely to occur after many less severe cases are chosen in the random sampling. This seemingly erratic pattern is shown well by our samples. An additional source of variation in our data was the pooling of all birds along one coast as a single sample; no doubt site differences in parasite loads confound our data. Samples as small as 6 birds characteristically approached the asymptotic diversity value, but in such small samples a bird with an atypical infestation could markedly increase or decrease the value. Thus, we are not entirely satisfied with the smaller pelican samples but think that they characterize the parasite communities reasonably well. Our smallest samples, as few as 2 birds, were judged to be inadequate. However, we include them in the results anyway, with trepidation. The endangered status of this bird made larger samples unjustifiable at the time of collection.

#### THE ORGANISMS

Like the declining Pacific coast subspecies, some eastern populations of the Brown Pelican also have declined recently. In Texas, only 18 young were produced in 1963

(Webster 1963). Indigenous wild pelicans have not nested in Louisiana since 1961, though pelicans brought to Louisiana from Florida as flightless nestlings in 1968, 1969, 1970, and 1971 nested when they were 3 years old (Williams and Joane 1974). Only 1 small colony exists in North Carolina (Wray and Davis 1959). In South Carolina the population apparently has declined, but this may be due to the gradual eroding of the nesting site at Deveaux Banks (T. A. Beckett, pers. comm. cited by Schreiber and Risebrough 1972). Pelicans have not been known to nest in Georgia (Burleigh 1958), Alabama (Imhof 1976), or Mississippi (Burleigh 1944) in recent years.

In the United States, only Florida has a stable population of Brown Pelicans. During 1968–74 biologists of the Florida Game and Fresh Water Fish Commission made visits and aerial surveys of all colonies in the state. Nesting occurred in 30 colonies; all but one colony (at Port St. Joe) were on islands off the Florida peninsula. There appeared to be a relatively stable population of between 11,000 and 16,000 adult pelicans (Williams and Martin 1968, 1970; Nesbitt *et al.* 1977).

Thirty-one species of helminths were found in the pelicans (Courtney and Forrester 1974). Most were rare, contributing importantly to the diversity of the helminth community but having minor impact on the health of the host. Only 6 species were frequent enough to be considered as consistently dominant community members. One of these inhabited the proventriculus, 4 the small intestine, and 1 the kidneys. Most of these helminths enter the pelicans as intermediate forms within ingested food. These then mature into adult forms of the parasites. An exception to this pattern is *Contraecaecum*, which enters both as an intermediate form as above and as an adult, by direct transfer from parent pelicans by regurgitative feeding of nestlings.

*Contraecaecum multipapillatum* and *C. spiculigerum* (Nematoda: Heterocheilidae; treated as 1 taxon hereafter) live in the proventriculus, where they may be free or attached to the mucosa. The life cycles of several species of *Contraecaecum* were determined by Huizinga (1965). Eggs hatch into ensheathed second stage larvae in 5 to 7 days. Larvae of both species infect transport hosts, the copepods *Trigriopus californicus* and *Cyclops vernalis*. *C. multipapillatum* requires a transport host, but the cosmopolitan *C. spiculigerum* can directly infect the intermediate hosts, fish. Larvae hatch and molt to the third stage in the intermediate hosts, a guppy (*Lebistes reticulatus*) and a killifish (*Fundulus heteroclitus*). After ingestion by the pelican, *Contraecaecum* undergo no tissue migration and survive about 90 days (Huizinga 1971).

The 4 most common parasites of the small intestine were the trematodes *Mesostephanus appendiculatooides* (Cyathocotyliidae); *Phagicola longus*, *P. sp. cf. minutus*, and *Galactostomum darbyi* (Heterophyidae); and *Stephanoprora denticulata* (Echinostomatidae).

The Brown Pelican is the only known final host of *M. appendiculatooides*. The first intermediate host is the marine snail, *Cerithium muscarum*, and the second intermediate hosts are mullet, *Mugil* spp. Pelicans become infected by eating mullet (Hutton and Sogandares-Bernal 1960a).

The most abundant and ubiquitous helminth found in this study was the trematode, *Phagicola longus*. The first intermediate host is unknown but may be a hydrobiid snail (R. W. Heard, pers. comm.). The second intermediate hosts are mullet, in which metacercaria inhabit the heart muscle in great numbers and less commonly the intestinal wall and muscle (Hutton and Sogandares-Bernal 1959). *Phagicola* undergo a brief tissue migration in the intestine of the Brown Pelican (Ciurea 1924).

The life cycle of *G. darbyi* is unknown. Mature *S. denticulata* occur in several species of water birds in Florida (Courtney 1973). The metacercariae have been found (Stunkard and Uzman 1962) in a killifish, *Fundulus heteroclitus*.

TABLE 1  
SAMPLING PARAMETERS, DIVERSITY, AND EQUITABILITY OF HELMINTH COMMUNITIES FROM  
FLORIDA AND LOUISIANA

	No. of Pelicans	No. of Parasite Species	No. of Parasite Individuals	No. of Parasites/ Bird	H'	E
<b>Total Pelicans</b>						
Florida, Louisiana	106	28	756,238	7,134	0.640	0.192
<b>Fledged</b>						
Florida Atlantic coast	39	20	391,159	10,030	0.458	0.143
Florida Gulf coast	14	15	73,472	5,248	0.864	0.319
Louisiana coast	14	12	167,843	11,989	0.074	0.030
<b>Florida Atlantic coast</b>						
Nestlings 4.5 weeks	2	7	2,171	1,086	0.876	0.450
Nestlings 7 weeks	3	5	7,778	2,593	0.705	0.438
Nestlings 9 weeks	4	9	27,922	6,980	0.704	0.361
Fledged young (12- 52 weeks)	5	14	50,183	10,037	0.321	0.122
Subadults (1-3 years)	27	18	271,895	10,070	0.436	0.151
Adults (>3 years)	7	17	69,083	9,869	0.390	0.138
<b>Florida Gulf coast</b>						
Nestlings 2 weeks	6	4	1,094	182	0.071	0.051
Nestlings 3 weeks	6	4	3,180	530	0.107	0.077
Nestlings 4.5 weeks	6	9	14,002	2,334	0.676	0.308
Nestlings 7 weeks	6	8	28,836	4,806	0.500	0.240
Nestlings 9 weeks	6	10	26,044	4,341	0.961	0.417
Fledged young (12- 52 weeks)	3	11	25,471	8,490	0.224	0.093
Subadults (1-3 years)	4	12	21,801	5,450	1.095	0.440
Adults (>3 years)	7	13	26,199	3,743	0.959	0.374
<b>Louisiana coast</b>						
Fledged young (12- 52 weeks)	3	7	56,915	18,972	0.120	0.062
Subadults (1-3 years)	5	7	66,988	13,398	0.034	0.017
Adults (>3 years)	6	10	43,935	7,322	0.062	0.027

The kidney fluke, *Renicola thapari*, is found in both Brown and White pelicans (*Pelecanus erythrorhynchos*; Courtney 1973). Its life cycle is unknown.

#### RESULTS

The diversity of Brown Pelican helminth communities (Table 1) was very low in all cases. Values for fledged birds ranged from 0.074 to 0.864. High-

TABLE 2

CONTRIBUTION TO COMMUNITY DIVERSITY ( $H'N$ ) OF ECOLOGICALLY DOMINANT HELMINTHS<sup>1</sup>

Location	2 Weeks	3 Weeks	4.5 Weeks	7 Weeks	9 Weeks	Fledged Young	Sub-adults	Adults
<b>Florida Gulf coast</b>								
<i>M. appendiculatoides</i>	.012*	.020*	.228*	.123*	.348	.082	.367	.368
<i>P. longus</i>	—	—	.345	.222	.288*	.040*	.334*	.313*
<i>G. darbyi</i>	.006	.006	.014	.006	.004	.024	.062	.042
<i>S. denticulata</i>	—	—	.002	.001	.006	TR <sup>1</sup>	.002	.004
<i>Contracaecum</i> spp.	.046	.074	.050	.075	.148	.022	.066	.059
<i>R. thapari</i>	.006	.006	.032	.072	.164	.047	.207	.080
<b>Florida Atlantic coast</b>								
<i>M. appendiculatoides</i>			.349*	.367	.314	.210	.140	.246
<i>P. longus</i>			.355	.307*	.214*	.085*	.089*	.110*
<i>G. darbyi</i>			—	—	—	—	.024	—
<i>S. denticulata</i>			—	—	—	.009	.021	.012
<i>Contracaecum</i> spp.			.089	.028	.166	.008	.015	.008
<i>R. thapari</i>			—	—	TR <sup>1</sup>	.002	.006	.002
<b>Louisiana coast</b>								
<i>M. appendiculatoides</i>						—	—	TR <sup>1</sup>
<i>P. longus</i>						.023*	.005*	.009*
<i>G. darbyi</i>						—	TR <sup>1</sup>	—
<i>S. denticulata</i>						.082	.014	.033
<i>Contracaecum</i> spp.						.010	.014	.009
<i>R. thapari</i>						—	—	—

<sup>1</sup> TR = presence in trace amounts.\*  $H'n_1 < H'n_2$ .

est diversity was 1.095 in subadults from the Florida Gulf coast, and the least diverse sample was 0.034, subadults from the Louisiana coast. Such low diversities are comparable to those found in the benthic macroinvertebrates of polluted streams (Wilhm 1970b). Equitability values also were very low—0.45 for the most equitable sample.

The reason for this low diversity and inequitable distribution of relative abundances is that every sample was dominated by a superabundant species ( $H'n_1 < H'n_2$ , Table 2), either *M. appendiculatoides* or *P. longus*. The former species invades nestlings and is superabundant during the early weeks, but at 7 to 9 weeks of age *P. longus* populations become dominant and superabundant. Other flukes of the small intestine, *G. darbyi* and *S. denticulata*, were consistent though minor members of the helminth communities. These were most important in fledged birds. *S. denticulata* was most im-

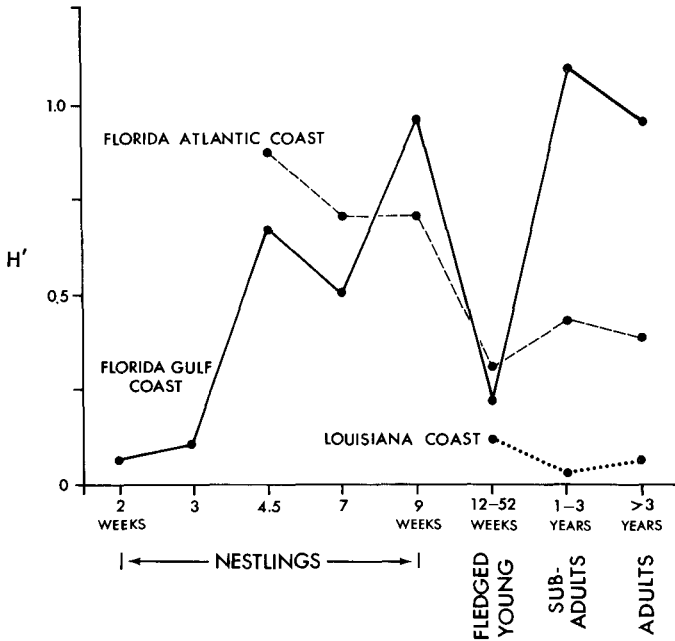


FIG. 1. Diversity of helminth communities in seral ages of the Brown Pelican.

portant in Louisiana pelicans, from which *M. appendiculatoides* was absent.

Change of diversity during community succession (Fig. 1) deviated from the expected pattern of increase with seral age. Diversity increased from young to older nestlings, decreased markedly in fledged young, increased again in the subadult years, and then dropped slightly in sexually mature birds. However, no increase in diversity occurred in subadult and adult birds from the Louisiana coast. Probably these changes correspond with major events in the life history of the host. Helminth communities in subadult and adult pelicans differed distinctly among the 3 regions, with highest diversity at the Florida Gulf coast and lowest at the Louisiana coast. A striking measure of the low diversity in Louisiana birds was the absence of 10 parasite species that occurred in Florida birds (Courtney and Forrester 1974).

The main features of parasite community succession are shown in Fig. 2. Most parasite species were very rare, and only *M. appendiculatoides*, *P. longus*, and *Contracaecum* occurred in numbers large enough to illustrate ecological processes.

*M. appendiculatoides* in the Florida Gulf coast comprised almost all of the parasite infection of 2-week-old pelicans, with abundance not exceeding

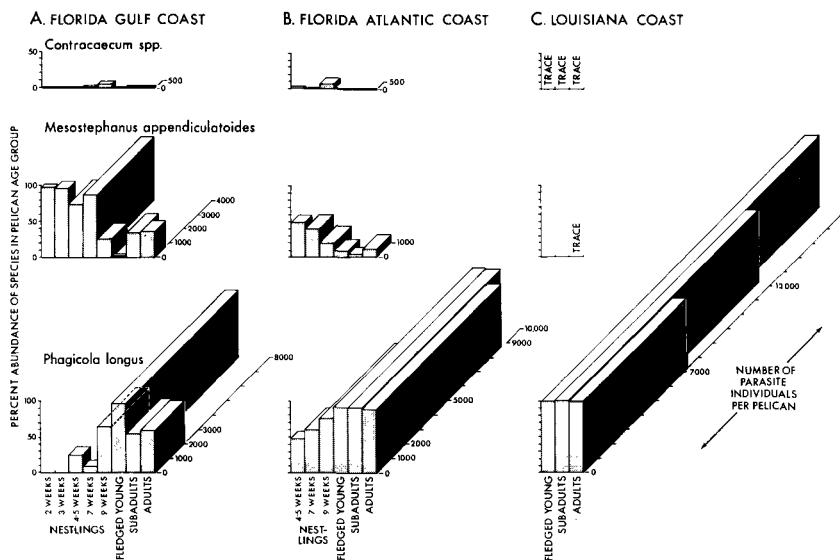


FIG. 2. Frequency and number of the most abundant helminths in Brown Pelicans from three regions. Bars show the major features of parasite community succession as a function of host age.

about 500 per bird. The importance of this fluke remained high and loads increased to 4000 per bird at 7 weeks. Frequency and numbers decreased to insignificant levels in fledglings and then increased to moderate proportions in subadults and adults, with about 1000 per bird. Among Florida Atlantic coast birds, *M. appendiculatoides* infections remained at about 1000 per bird from nestlings to adults, with relative abundance diminishing from moderate to low levels as other parasites became more common. In Louisiana, *M. appendiculatoides* was absent from fledged young and subadults and occurred in very small numbers among adults.

*P. longus* was absent from young nestlings but occurred as up to half the total parasites and 1000 per bird when nestlings were 4-5 weeks old. This fluke quickly reached enormous numbers, up to 8000 per bird on the Florida Gulf coast, 10,000 on the Florida Atlantic coast, and over 18,000 on the Louisiana coast. In all cases, the largest populations occurred among fledged young, with a decrease in subadult and adult classes. Infections were slightly lower (9000 per adult) on the Atlantic coast but were reduced substantially (2000 per adult) along the Florida Gulf coast.

*Contracaecum* was a minor community member in birds of both young

and older age classes but consistently developed small populations in all 9-week-old nestlings. These populations nearly disappeared after birds were fledged.

#### DISCUSSION

Low diversities and the superabundance of *M. appendiculatoides* and *P. longus* show that few parasites are well adapted to exploit the pelican resource. Of the 2 that are highly successful, *M. appendiculatoides* is specific to Brown Pelicans as a final host, whereas *P. longus* occurs also (Hutton and Sogandares-Bernal 1960b) in the Great Egret, *Casmerodius albus*. Host generalists such as *S. denticulata* do not achieve large populations in the Brown Pelican.

*Zoogeography.*—Effects of zoogeographic processes are evident from an unintentional faunistic “experiment.” Between 1958 and 1961 the last nesting Brown Pelicans in Louisiana were extirpated. In 1968 and subsequent years, 12-week-old nestlings were introduced from colonies on the Atlantic coast of Florida. These birds were fed at the release site to enhance survival, and they were not chemically treated to eliminate parasites. The new pelican population began to reproduce in 1971.

The low helminth diversity found in Louisiana may have resulted from this history of extirpation and reintroduction. Several of the parasites expected in pelicans probably became rare or extirpated during the years when pelicans were absent from this region. Introduced birds probably brought *M. appendiculatoides* with them, and adults now include a few in their internal faunas. However, the life cycle appears to have been broken by the loss of intermediate forms of *M. appendiculatoides* in Louisiana mullet, and the few adult flukes introduced in infected birds may be insufficient to re-establish a complete life cycle. The kidney fluke *R. thapari* is now absent from Louisiana, though present in some numbers in the Florida portion of the Gulf coast. Other helminths present on either coast of Florida but absent off Louisiana include *Cyathostoma phenisci*, *Capillaria* sp. cf. *mergi*, *Galactostomum fregatae*, *G. darbyi*, *Echinochasmus* sp. cf. *dietzevi*, *Austroilharzia terrigalensis*, *Carneophallus turgidus*, *Parvitaenia ibisae*, and an unidentified schistorophid larva.

By contrast, Louisiana pelicans had vast numbers of *P. longus*. This fluke no doubt persisted in Louisiana during the pelicans’ absence, inasmuch as an alternate final host (the Great Egret) was present continuously.

The other striking regional difference in diversity is in adult pelicans, which have relatively diverse parasite communities on the Florida Gulf coast but comparatively poor communities on the Atlantic coast (Table 1). Though



this pattern probably reflects a fundamental difference in pelican habitat in the 2 areas, we cannot determine its nature. Because the parasites are acquired from fish, it seems reasonable to suppose that the 2 coasts differ substantially in the relative abundance of fish taxa used as food or that environmental factors cause contrasting phenologies of fish reproduction and movement.

*Food web interactions.*—Though actual changes in diet as pelicans become older are unstudied, changes in parasite communities derived from food organisms indicate several dietary patterns. The observed increase in helminth diversity with advancing age of pelican nestlings would be expected if birds progressively feed on larger fish of greater taxonomic diversity. Sharp decline of diversity in fledglings occurs when young birds are learning to feed themselves, so food intake may be low or concentrated on a few prey species. This diversity change results from explosive growth of *P. longus* populations, indicating heavy dependence on mullet (the second intermediate host) as food during this period.

The decline of *Contracaecum* in fledgling pelicans probably reflects prey selection by the fledglings in place of selection by parent birds. Because these parasites survive only about 90 days (Huizinga 1971), their numbers depend on continual ingestion of infected hosts. An age immunity effect may also reduce the parasite numbers.

*Competition.*—The unusually depauperate helminth community in Louisiana pelicans reveals patterns (Fig. 2) from which we infer the importance of interspecific competition among parasites. The Louisiana samples contain almost no *M. appendiculatoides* but enormous numbers of *P. longus*. In contrast, Florida birds are infected with moderate *M. appendiculatoides* populations and substantially smaller *P. longus* populations. We interpret the success of *P. longus* in Louisiana birds as attributable to lack of interspecific competition from *M. appendiculatoides*. Both trematodes occupy the same portion of the small intestine, and *M. appendiculatoides* is about 3 times as large as *P. longus*, so the former should have an energetic impact that is disproportionate to its numbers.

Another intestinal trematode, *S. denticulata*, also is more abundant (48 flukes per adult bird) in Louisiana than in Florida. This fluke is about 10 times the size of *P. longus*. Again, we judge the success of *S. denticulata* in Louisiana pelicans to result from low competition in the absence of *M. appendiculatoides*. Our interpretation is further supported by the observations that *S. denticulata* is rare (2 flukes per adult) in Florida Gulf coast pelicans, in which *M. appendiculatoides* is most numerous, but is more common (19

flukes per adult) in Florida Atlantic coast pelicans having fewer *M. appendiculatoides*.

Similarly, the reduction of *M. appendiculatoides* in pelicans of both Florida coasts probably results from competition with *P. longus*. These 2 undergo a shift in dominance that is evident in the 7 and 9 week stages in Fig. 2 and Table 2.

Presumably competition among flukes in the more diverse Florida communities operates by reducing the survival rates of parasites after they have been ingested. Importantly, such competition also indicates the likelihood of competition between parasites and the host birds for some nutrients.

*Development of immunity by the host.*—Eventual decline of *P. longus* populations in adult pelicans (Fig. 2) may reflect development of age immunity, for no other small intestinal parasites remain abundant, so the decline cannot be attributed to competition. Differences in the amount of decline of this parasite among pelican populations may be explained by differences in parasite loads established in fledglings and differing levels of competition from *M. appendiculatoides*, especially during the subadult years. *P. longus* metacercaria from mullet must encyst in pelican intestinal mucosa in order to mature. During this brief tissue-dwelling stage they make a good target for an immunological response by the host. Parasites like *M. appendiculatoides*, which apparently remain in the lumen without entering intestinal tissue, offer less opportunity for immunological counter-measures.

An alternative explanation (which we cannot evaluate) of the *P. longus* decline is that pelicans surviving longest and thus best represented in the adult age class are those that avoid mullet in their diets.

*Management.*—Heavy infection of Louisiana pelicans by *P. longus* might be a serious problem worth avoiding in future reintroduction efforts. A factor probably contributing to the imbalance between *P. longus* and *M. appendiculatoides* was that introduced birds came from the Atlantic coast of Florida, where considerable imbalance prevailed (Fig. 2). Pelicans from the Gulf coast of Florida, in which both of these trematodes have reached moderate numbers and evidently balanced populations, may be more fit candidates for reintroduction.

#### SUMMARY

Helminths from *Pelecanus occidentalis* were described as communities of several successional ages and of 3 geographic regions. Community diversity was uniformly low, resulting from enormous numbers of *Mesostephanus appendiculatoides* in young hosts and *Phagicola longus* in old birds. Regional differences in diversity are attributed to unknown features of pelican habitat along Florida coasts and a history of pelican

extirpation and reintroduction on the Louisiana coast, which appears to have caused extirpation of some parasite taxa. Seral changes in parasites indicate increasing diversity of food items as nestlings grow, sudden heavy feeding on mullet (*Mugil* spp.) at fledging, and apparent avoidance of other fish species by fledged birds. The success of *P. longus* populations in Louisiana birds is attributed to a lack of interspecific competition from *M. appendiculatoides*. Eventual decline of *P. longus* populations in adult pelicans may reflect development of age immunity, though other explanations are possible. Success of efforts to reintroduce pelicans into formerly occupied range may be enhanced by selecting birds with balanced parasite communities.

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