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Comparison of Helminths of Rice Rats, *Oryzomys palustris,* from Freshwater and Saltwater Marshes in Florida[1]

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ABSTRACT: Examination of 288 rice rats, *Oryzomys palustris,* collected in Florida over a 2-yr period revealed 45 species of helminth parasites: 4 cestodes, 21 trematodes, and 20 nematodes. Rats from a freshwater marsh harbored 20 species (3 cestodes, 2 trematodes, 15 nematodes), whereas those from a saltwater marsh had 40 species (3 cestodes, 20 trematodes, 17 nematodes), with 15 species shared between marshes (2 cestodes, 1 trematode, 12 nematodes). Microphallid trematodes (10 species) dominated the fauna in the saltwater marsh, and nematodes (15 species) dominated in the freshwater marsh. Prevalence and intensity of infection of shared nematode species were reduced greatly in rats from the saltwater marsh. The fauna of the omnivorous rice rat was characterized by heteroxenous species. Known life cycles and feeding experiments indicated that rice rats ate tadpoles, frogs, insects, and land snails in the freshwater marsh, and crabs, fish, aquatic snails, and insects in the salt marsh. The rice rat shared helminth species with the cotton rat (*Sigmodon hispidus*), round-tailed muskrat (*Neofiber alleni*), opossum (*Didelphis virginiana*), raccoon (*Procyon lotor*), and clapper rail (*Rallus longirostris*).

KEY WORDS: rice rat, *Oryzomys palustris,* survey, Florida, helminths, freshwater marsh, salt marsh, intermediate hosts, prevalence, intensity.

Rice rats, *Oryzomys palustris* (Harlan), inhabit both inland freshwater marshes and coastal salt marshes of the southeastern United States. They occupy an unusual trophic niche for a rodent, feeding on insects, snails, crabs, and fish (Negus et al., 1961; Sharp, 1967), as well as preying on the eggs and nestlings of marsh birds (Post, 1981). Because the literature on the helminth fauna of the rice rat consisted only of scattered records, a study was initiated in Florida in April 1970.

As a result of this study, 6 new species of nematodes (*Parastrongylus schmidti, Hassalstrongylus forresteri, Hassalstrongylus lichtenfelsi, Litomosoides scotti, Syphacia oryzomyos, Capillaria forresteri*), and 1 new species of trematode (*Lyperosomum intermedium*) have already been described (see Kinsella, 1971; Denton and Kinsella, 1972; Quentin and Kinsella, 1972; Forrester and Kinsella, 1973; Durette-Desset, 1974; Kinsella and Pence, 1987). In addition, the rice rat was found to be the first known natural definitive host for 2 other trematodes (*Stictodora cursitans, Catatropis johnstoni*), and the life cycles of these trematodes have been described (see Bush and Kinsella, 1972; Kinsella and Heard, 1974).

The purpose of the present paper is to compare the helminth fauna of rice rats from freshwater and saltwater marshes in Florida.

Materials and Methods

Rats were live-trapped in Sherman traps at 3-mo intervals between April 1970 and May 1972. Ages were determined on the basis of weight and pelage. The ecosystem of the freshwater marsh, Paynes Prairie, near Gainesville, Alachua County, has been described extensively by Birkenholz (1963). A typical *Juncus-Spartina* saltwater marsh on Waccasassa Bay near Cedar Key, Levy County, was also trapped. The ecosystem of this area was described by Post (1981).

Rats were brought to the laboratory and killed immediately before examination. Methods of collecting, fixing, and staining helminths have been described by Kinsella (1974). When trematodes were very abundant, their numbers were estimated by mixing thoroughly with 250 ml of water and counting a 10-ml aliquot.

In order to determine the intermediate hosts of some trematodes in the salt marsh, various invertebrates were fed to laboratory-born rice rats obtained from pregnant females captured on Paynes Prairie. Later these rats were killed and examined for trematodes by the same methods. Intermediate hosts from Cedar Key were also dissected and examined for metacercariae.

Chi-square and Mann-Whitney *U*-tests were used to determine significant differences ($P < 0.05$) in prevalence and intensity, respectively, with regard to sex, age, and locality of hosts.

Results

Forty-five species of helminths (4 cestodes, 21 trematodes, 20 nematodes) were found. Table 1 lists the site, prevalence, and intensity of infection of each species. Rats from Paynes Prairie

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Table 1. Helminth parasites of *Oryzomys palustris* from freshwater and saltwater marshes in Florida.

	Fresh water (N = 178)			Salt water (N = 110)		
	Prevalence (%)	Intensity		Prevalence (%)	Intensity	
		Mean	(Range)		Mean	(Range)
Cestoda						
Hymenolepis diminuta (Rudolphi, 1819) (3)*	19	4	(1–15)	1	1	(1)
Taenia rileyi Loewen, 1929 (8)	0	—	—	1	2	(2)
Taenia mustelae Gmelin, 1790 (8)	0.5	†	†	0	—	—
Cladotaenia circi Yamaguti, 1935 (8)	0.5	†	†	1	†	†
Trematoda						
Microphallus basodactylophallus (Bridgman, 1969) (3)	0	—	—	94	‡	‡
Microphallus nicolli (Cable and Hunninen, 1938) (3)	0	—	—	9	‡	‡
Microphallus sp. (3)	0	—	—	10	‡	‡
Maritrema prosthrometra Deblock and Heard, 1969 (3)	0	—	—	5	‡	‡
Maritrema sp. I (3)	0	—	—	69	‡	‡
Maritrema sp. II (3)	0	—	—	19	‡	‡
Probolocoryphe glandulosa (Coil, 1955) (3)	0	—	—	56	‡	‡
Gynaecotyla adunca (Linton, 1905) (3)	0		—	15	‡	‡
Levinseniella sp. (3)	0	—	—	49	‡	‡
Odhneria odhneri Travassos, 1921 (3)	0	—	—	6	‡	‡
Ascocotyle angrense Travassos, 1916 (3)	0	—	—	25	‡	‡
Ascocotyle mollienisicola (Sogandares-Bernal and Bridgman, 1960) (3)	0	—	—	9	‡	‡
Stictodora cursitans (Holliman, 1961) (3)	0	—	—	52	36	(1–100)
Parvatrema sp. (3)	0	—	—	26	‡	‡
Lyperosomum intermedium Denton and Kinsella, 1972 (6)	0	—	—	45	20	(1–50)
Zonorchis komareki (McIntosh, 1939) (7)	0	—	—	1	1	(1)
Echinochasmus schwartzi Price, 1931 (3)	0	—	—	19	4	(1–15)
Catatropis johnstoni Martin, 1956 (4)	0	—	—	30	91	(1–500)
Urotrema scabridum (Braun, 1900) (3)	0	—	—	23	8	(1–25)
Brachylaeme virginianum (Dickerson, 1930) (3)	15	5	(1–23)	0	—	—
Fibricola lucida (LaRue and Bosma, 1927) (3)	67	143	(1–1,975)	11	17	(1–65)
Nematoda						
Capillaria hepatica (Bancroft, 1893) (5)	8	†	†	6	†	†
Capillaria gastrica Baylis, 1926 (1)	4	1	(1–2)	6	4	(1–10)
Capillaria forresteri Kinsella and Pence, 1987 (2)	46	10	(1–50)	1	1	(1)
Strongyloides sp. (3)	30	4	(1–30)	0	—	—
Monodontus sp. (3)	0	—	—	1	1	(1)
Hassalstrongylus spp.§ (3)	92	99	(1–515)	9	11	(1–75)
Trichostrongylus sigmodontis Baylis, 1945 (3)	8	4	(1–15)	3	2	(1–4)
Trichostrongylus affinis Graybill, 1924 (4)	14	3	(1–14)	6	7	(1–19)
Parastrongylus schmidti (Kinsella, 1971) (9)	7	4	(1–20)	3	3	(1–8)
Syphacia oryzomyos Quentin and Kinsella, 1972 (4, 5)	42	34	(1–275)	0	—	—
Physaloptera hispida Schell, 1952 (2)	35	14	(1–92)	0	—	—
Physaloptera sp. (2)	0	—	—	4	2	(1–2)
Mastophorus muris (Gmelin, 1790) (2)	36	6	(1–70)	1	1	(1)
Pterygodermatites spp.‖ (3)	20	3	(1–9)	5	3	(1–12)
Skrjabinoclava thapari deFrietas, 1953 (2)	0	—	—	28	4	(1–10)
Larval spirurid (2, 3, 4)	0	—	—	5	2	(1–5)
Litomosomoides scotti Forrester and Kinsella, 1973 (10, 11)	0	—	—	57	12	(1–104)

* Location in host: (1) gastric mucosa, (2) stomach cavity, (3) small intestine, (4) cecum, (5) large intestine, (6) pancreatic duct, (7) bile duct, (8) liver mucosa, (9) pulmonary arteries, (10) abdominal cavity, (11) pleural cavity.

† Not counted.

‡ Individual counts of microphallids, gymnophallids, and heterophyids not made. Total numbers ranged from 40 to 30,000/rat (mean 4,050).

§ A complex of 3 species, *H. musculi* (Dikmans, 1935), *H. forresteri* Durette-Desset, 1974, and *H. lichtenfelsi* Durette-Desset, 1974. Females cannot be distinguished so data were combined.

‖ Two species, *P. ondatrae* (Chandler, 1941) and *P.* sp. Females cannot be distinguished so data were combined.

were infected with 3 cestodes, 2 trematodes, and 15 nematodes, whereas those from Cedar Key were infected with 3 cestodes, 20 trematodes, and 17 nematodes. Fifteen of the 45 species were shared between rats from the 2 marshes (2 cestodes, 1 trematode, 12 nematodes).

The number of helminth species per infected host in the freshwater marsh varied from 1 to 11 (mean 6.1, median 6). In the salt marsh, the number of species varied from 2 to 16 (mean 8.4, median 8). No rice rat was helminth free. Representative specimens were deposited in the U.S. National Parasite Collection in Beltsville, Maryland: Nos. 71579 (*P. schmidti*), 63079 (*S. oryzomyos*), 72288 (*L. scotti*), 72799 (*S. cursitans*), 73424 (*C. forresteri*), 79871 (*Hassalstrongylus* spp.), and 79872 (mixed microphallids and heterophyids).

Cestodes

The only adult tapeworm encountered was *Hymenolepis diminuta,* a common parasite of rodents in the United States (Doran, 1954). Prevalence was high on Paynes Prairie, but only 1 rat was infected at Cedar Key with a single worm. Individual infections were found of larval *Taenia rileyi,* a parasite of bobcats; *Taenia mustelae,* a parasite of skunks and other mustelids; and *Cladotaenia circi,* a parasite of hawks.

Trematodes

Only 1 trematode, *Fibricola lucida,* was recorded from rats in both types of marsh. Both prevalence and intensity of infection were significantly higher on Paynes Prairie. The genus *Fibricola* uses tadpoles and frogs as the infective intermediate hosts (Chandler, 1942). *Brachylaeme virginianum* was found only on Paynes Prairie and uses land snails as second intermediate hosts (Krull, 1934).

The remaining 19 species of trematodes were found only in rats from Cedar Key. Ten of these species belong to the family Microphallidae, a group possessing precocious metacercariae that may already be producing eggs in the intermediate host. These minute trematodes show little host specificity and are common parasites of various marine mammals and shore birds. *Microphallus* sp. and *Maritrema* sp. I are the same undescribed species reported by Heard (1970) in clapper rails (*Rallus longirostris*) from the Atlantic and Gulf Coasts. *Maritrema* sp. II and *Levinseniella* sp. apparently are undescribed species.

Feeding experiments established the following as intermediate hosts of microphallids at Cedar Key: *Uca rapax* (fiddler crab)—*Gynaecotyla adunca, Probolocoryphe glandulosa, Microphallus* sp.; *Uca pugilator* (fiddler crab)—*Maritrema prosthrometra, Maritrema* sp. I. and II, *Levinseniella* sp.; *Callinectes sapidus* (blue crab)—*Microphallus basodactylophallus*; *Eurytium limosum* (stone crab)—*Microphallus nicolli.* Up to 30,000 microphallids were present in individual rats, with *M. basodactylophallus* and *Maritrema* sp. I and II predominating over other species by a ratio of 20 to 1.

An undescribed gymnophallid, *Parvatrema* sp., was present in small numbers. This was confirmed as the *Parvatrema* sp. II reported by Heard (1970) in clapper rails (Heard, pers. comm.). One rice rat fed several snails, *Melampus coffeus,* from Cedar Key was found infected with 125 flukes of this species.

The life cycle of *Stictodora cursitans* at Cedar Key was reported by Kinsella and Heard (1974). Killifish, *Fundulus* spp., were found infected with the metacercariae. *Fundulus* spp. have also been reported as the intermediate hosts of *Ascocotyle angrense* and *Echinochasmus schwartzi* (Sogandares-Bernal and Lumsden, 1963; Heard, 1970), recorded here for the first time from rice rats. The intermediate hosts of *Ascocotyle mollienisicola* are small fish called mollies, of the genus *Mollienisia* (Sogandares-Bernal and Bridgman, 1960).

Bush and Kinsella (1972) found the intermediate host of *Catatropis johnstoni* at Cedar Key to be the snail, *Cerithidea scalariformis.* Although the cercariae can encyst on vegetation, they showed an affinity for encysting on the snail's operculum, so the rice rat may be infected by eating the snail rather than vegetation.

Urotrema scabridum has been reported from bats (*Molossus* sp.) in Brazil and muskrats (*Ondatra zibethicus*) in Maryland (Penner, 1941) and commonly infected the rice rat at Cedar Key. An insect intermediate host may be the link between infections in these 2 disparate groups of mammals.

Nematodes

Although more species of nematodes (17) were found in rice rats at Cedar Key than at Paynes Prairie (15), prevalence and intensity of infection in 8 of 12 of the shared species were significantly lower in the salt marsh (see Table 1). Three species (*Strongyloides* sp., *Syphacia oryzomyos, Physa-*

Table 2. Prevalence and intensity of nematode infections with regard to sex and age of host.

Locality and species	Juveniles		Subadults and adults		Males		Females	
	Prevalence (%)	Intensity mean	Prevalence (%)	Intensity mean	Prevalence (%)	Intensity mean	Prevalence (%)	Intensity mean
Freshwater marsh								
Capillaria forresteri	4	1	52*	10*	45	10	46	9
Parastrongylus schmidti	0	—	8*	7*	5	6	10	2
Pterygodermatites spp.	4	1	23*	3	21	3	18	3
Mastophorus muris	4	5	25*	6	40	17	25*	5*
Physaloptera hispida	7	1	41*	14*	33	6	40	7
Syphacia oryzomyos	37	7	43	33*	53	37	24*	21*
Saltwater marsh								
Pterygodermatites spp.	0	—	7*	3*	4	5	7	1
Litomosoides scotti	44	11	73*	13	66	11	44	16

* Significant difference ($P < 0.05$).

loptera hispida) were found only at Paynes Prairie, and 4 species were restricted to the salt marsh (*Monodontus* sp., *Skrjabinoclava thapari, Litomosoides scotti,* and in an unidentified larval spirurid). The larval spirurid was found in dissections of fiddler crabs, *Uca rapax* and *Uca pugilator,* and may be a parasite of birds that does not mature in rice rats. Larvae thought to be the infective stages of *S. thapari* were found in the same 2 species of crabs, but their identity was not confirmed by infecting laboratory-born rats.

Only nematodes showed significant differences in prevalence or intensity of infection according to sex or age of the host (Table 2). On Paynes Prairie, 3 nematodes (*Capillaria forresteri, Parastrongylus schmidti, P. hispida*) were higher in prevalence and intensity in adults and subadults than in juveniles, 3 (2 species of *Pterygodermatites* and *Mastophorus muris*) were higher in prevalence but not in intensity, and 1 (*S. oryzomyos*) was higher in intensity, but not in prevalence. At Cedar Key, *Pterygodermatites* spp. were found only in adults, whereas *L. scotti* was higher in prevalence, but not intensity, in adults. *Mastophorus muris* and *S. oryzomyos* had a significantly higher prevalence and intensity in male rats.

Discussion

The presence of 45 species of helminths, and, more specifically, 21 species of trematodes in a rodent is unprecedented and certainly is related to both the diversity of habitat and unique food habits of the rice rat. The trematode fauna especially reflected the omnivorous diet. Intermediate hosts confirmed here by dissection or feeding experiments included fiddler crabs, blue crabs, stone crabs, killifish, mollies, and aquatic snails. Other food items indicated from known life cycles of trematodes are tadpoles, frogs, and land snails.

Prevalence and intensity of infection of trematodes in rats from the salt marsh indicated that virtually 100% of rice rats have a carnivorous diet. In the freshwater marsh, the high prevalence of *F. lucida* showed that tadpoles and frogs are an important component of the diet, and the prevalence of 4 nematodes (*P. hispida, M. muris, Pterygodermatites* spp.) and 1 cestode (*H. diminuta*) indicated that insects may take the place in the diet of crabs in rats from the salt marsh.

The fauna of the rice rat in the freshwater marsh was dominated by nematodes, both in number of species present and total helminth burden. Monoxenous nematodes (*Strongyloides* sp., *Hassalstrongylus* spp., *Trichostrongylus sigmodontis, T. affinis*) were absent or greatly reduced in prevalence in the salt marsh, where the brackish environment may affect their larval development. Although the pinworm, *S. oryzomyos,* presumably is transmitted directly from host to host by the egg, infections were absent in rice rats from the salt marsh. Paradoxically, *Syphacia sigmodontis,* collected from the cotton rat (*Sigmodon hispidus*) from the same 2 marshes, had a much higher prevalence and intensity of infection in the salt marsh (Kinsella, 1974).

The acquisition of nematodes by young rice

rats showed that monoxenous species (*Strongyloides* sp., *Hassalstrongylus* spp., *Trichostrongylus* spp.) were acquired earliest, whereas heteroxenous species (*P. hispida, M. muris, Pterygodermatites* spp., *P. schmidti*) were acquired later. The prevalence of *L. scotti,* which is transmitted by a mite vector, was shown to increase directly with age (Forrester and Kinsella, 1973). Intensity of infection with *S. oryzomyos* also increased with age, although prevalence was not significantly different.

The pattern of acquisition of trematodes was less clear-cut. Because microphallids, gymnophallids, and heterophyids are precocious, and require very little development time within the definitive host, even the youngest rats collected in the salt marsh were infected with 1–4 species of trematodes. This indicated that their carnivorous diet may begin as soon as they leave the nest. Also, the time these trematodes live within the host is relatively short, so intensity of infection does not necessarily increase with age, but varies seasonally with availability of intermediate hosts (Heard, 1970).

The only other rodents trapped at Paynes Prairie were the cotton rat and the round-tailed muskrat (*Neofiber alleni*). At Cedar Key, the cotton rat was the only other rodent present. The rice rat shared 6 helminth species (1 cestode, 5 nematodes) with the cotton rat at Paynes Prairie, and 9 species (4 trematodes, 5 nematodes) at Cedar Key; and only 3 nematode species with the round-tailed muskrat (Kinsella, 1974; Forrester et al., 1987).

The rice rat also shared helminths with ecological associates such as the opossum, *Didelphis virginiana* (7 species), the raccoon, *Procyon lotor* (7 species), and the clapper rail (7 species) (see Harkema and Miller, 1964; Heard, 1970; Kinsella and Heard, 1974; Kinsella, unpubl. data), again primarily reflecting the lack of host specificity of the salt marsh trematodes.

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Literature Cited

Birkenholz, D. E. 1963. A study of the life history and ecology of the round-tailed muskrat (*Neofiber alleni* True) in north-central Florida. Ecological Monographs 33:187–213.

Bush, A. O., and J. M. Kinsella. 1972. A natural definitive host for *Catatropis johnstoni* Martin, 1956 (Trematoda: Notocotylidae), with notes on experimental host specificity and intraspecific variation. Journal of Parasitology 58:843–845.

Chandler, A. C. 1942. The morphology and life cycle of a new strigeid, *Fibricola texensis,* parasitic in raccoons. Transactions of the American Microscopical Society 61:156–167.

Denton, J. F., and J. M. Kinsella. 1972. *Lyperosomum intermedium* sp. n. (Trematoda: Dicrocoelidae) from the rice rat, *Oryzomys palustris,* from southeastern salt marshes. Journal of Parasitology 58:226–228.

Doran, D. J. 1954. A catalogue of the protozoa and helminths of North American rodents. II. Cestoda. American Midland Naturalist 52:469–480.

Durette-Desset, M. C. 1974. Nippostrongylinae (Nematoda: Heligmosomidae) nearctiques. Annales de Parasitologie Humaine et Compareé 49: 435–450.

Forrester, D. J., and J. M. Kinsella. 1973. Comparative morphology and ecology of two species of *Litomosoides* (Nematoda: Filarioidea) of rodents in Florida, with a key to the species of *Litomosoides* Chandler, 1931. International Journal for Parasitology 3:255–263.

———, **D. B. Pence, A. O. Bush, D. M. Lee, and N. L. Holler.** 1987. Ecological analysis of the helminths of round-tailed muskrats (*Neofiber alleni* True) in southern Florida. Canadian Journal of Zoology 65:2976–2979.

Harkema, R., and G. C. Miller. 1964. Helminth parasites of the raccoon, *Procyon lotor,* in the southeastern United States. Journal of Parasitology 50: 60–66.

Heard, R. W. 1970. Parasites of the clapper rail, *Rallus longirostris* Boddaert. II. Some trematodes and cestodes from *Spartina* marshes of the eastern United States. Proceedings of the Helminthological Society of Washington 37:147–153.

Kinsella, J. M. 1971. *Angiostrongylus schmidti* sp. n. (Nematoda: Metastrongyloidea) from the rice rat, *Oryzomys palustris,* in Florida. Journal of Parasitology 57:494–497.

———. 1974. Comparison of the helminth parasites of the cotton rat, *Sigmodon hispidus,* from several habitats in Florida. American Museum Novitates, No. 2540. 12 pp.

———, **and R. W. Heard.** 1974. Morphology and life cycle of *Stictodora cursitans* n. comb. (Trematoda: Heterophyidae) from mammals in Florida salt marshes. Transactions of the American Microscopical Society 93:408–412.

———, **and D. B. Pence.** 1987. Description of *Capillaria forresteri* sp. n. (Nematoda: Trichuridae) from the rice rat *Oryzomys palustris* in Florida, with notes on its ecology and seasonal variation. Canadian Journal of Zoology 65:1294–1297.

Krull, W. H. 1934. New experimental hosts for *Brachylaemus virginiana* (Dickerson) Krull. Journal of the Washington Academy of Sciences 24: 483–485.

Negus, N. C., E. Gould, and R. K. Chipman. 1961. Ecology of the rice rat, *Oryzomys palustris* (Harlan), on Breton Island, Gulf of Mexico, with a critique of the social stress theory. Tulane Studies in Zoology 8:95–123.

Penner, L. R. 1941. The status of *Urotrema shillingeri* Price, 1931 (Trematoda: Urotrematidae). Transactions of the American Microscopical Society 60: 359–364.

Post, W. 1981. The influence of rice rats *Oryzomys palustris* on the habitat use of the seaside sparrow *Amnospiza maritima*. Behavioral Ecology and Sociobiology 9:35–40.

Quentin, J. C., and J. M. Kinsella. 1972. Étude de trois espèces d'Oxyures *Syphacia* parasites de rongeurs Cricetides nord-americains. Hypotheses sur les filiations des espèces americaines. Annales de Parasitologie Humaine et Comparée 47:717–733.

Sharp, H. F. 1967. Food ecology of the rice rat, *Oryzomys palustris* (Harlan) in a Georgia salt marsh. Journal of Mammalogy 48:557–563.

Sogandares-Bernal, F., and J. F. Bridgman. 1960. Three *Ascocotyle* complex trematodes (Heterophyidae) encysted in fishes from Louisiana, including the description of a new genus. Tulane Studies in Zoology 8:31–39.

———, **and R. D. Lumsden.** 1963. The generic status of the heterophyid trematodes of the *Ascocotyle* complex, including notes on the systematics and biology of *Ascocotyle angrense* Travassos, 1916. Journal of Parasitology 49:264–274.