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Author: HENSLEY, MICHAEL S.

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PREVALENCE OF CUTEREBRID PARASITISM AMONG WOODMICE IN VIRGINIA

MICHAEL S. HENSLEY[1], Department of Zoology and Entomology, University of Tennessee, Knoxville, Tennessee 37916, USA.

Abstract: Botfly infestation was analyzed in 1319 small mammals from varied habitats and elevations in upland Virginia, 1972-1974. Adult *Cuterebra fontinella* were reared from bots infesting the woodmouse (*Peromyscus leucopus*). Of 651 woodmice, 199 (30.6%) were infested at least once. The season of bot infestation extended from May through November of all years, with peak prevalence (mean 42.2%) in August. Infestation in woodmice was general over a 2000 km^2 study area during peak months. Significantly greater prevalence ($P<0.001$) was seen in forested and brushy habitat (39.9%) compared with old fields (2.6%). Higher prevalence ($P<0.01$) was found in males than in females, and in postjuveniles compared to adults. Greatest overall prevalence (39.1%) was in postjuvenile males. Most warble sites (98%) were inguinal, and observations suggested that many infested adults were non-reproductive. Mean burden (1.27) was independent of host age, sex, habitat, and month of capture. Multi-infestations occurred in 23% of the affected mice; maximum burden was six bots. Botflies were absent or negligible in sympatric deermice (*P. maniculatus*) and twelve other species of rodents and shrews.

INTRODUCTION

Many species of rodents and lagomorphs are seasonally infested by larval botflies of the genus *Cuterebra* (Diptera: Cuterebridae). In contrast with most host-parasite interactions this infestation attracts special attention due to the large size of the larvae in relation to their relatively small hosts. Furthermore, larvae of many cuterebrid species typically migrate to encapsulation sites in the host's inguinal region.[7,8] This has caused some speculation about possible interference with host reproduction, and posed questions about the relationship between bot prevalence and host population dynamics.[24]

We now know much about the biology of adult and larval botflies of several species,[1,6,10,11] about physiological reactions of hosts to parasitism,[2,8,19,20] and about pathology of bot infestation.[4,19] However, there are many voids in our knowledge. Geographic ranges of the various botfly species are poorly known. Mammalogists commonly encounter bots during summer trapping, but few have reared adult flies for identification; thus, good host-parasite records are not available from many areas.[4] Little quantified evidence is available to identify which portions of host populations are most susceptible. Bot prevalence is known to vary according to habitat.[1,8,16] but there have been no reported statistical analyses of variations of prevalence in woodmice. Lastly, most previous studies were based on relatively small, localized samples. Any general conclusions about bot-host ecology drawn from such studies must necessarily be viewed with suspicion.

Unidentified warbles have been reported from Virginia in several studies,[15,18] and adult *C. buccata* were recently reared from bots infesting cottontails in Virginia.[13] However, there have been no reports of bot prevalence, infective season,

[1] Present address: Division of Science and Mathematics, Paul D. Camp Community College, Franklin, Virginia 23851, USA.

rearing of adult flies, or varying prevalence by habitat for rodent bots from Virginia or the adjacent Central Appalachians. Summarized herein is a study of botfly parasitism in the woodmouse (*Peromyscus leucopus noveboracensis*), with statistical analysis of data drawn from large samples stratified by host age, sex, habitat, and parasite burden. Also reported are additional notes concerning the biology of the parasite, its effects on the host population, and occurrence on incidental host species.

METHODS

Small mammals were captured and examined as a part of research on fox predation in upland Virginia (1972-1974), during which 1319 rodents and shrews were captured on permanent grids and temporary assessment traplines. Random 1 ha grids (Sherman traps, 16 m spacing) were maintained on each of four 10 ha woodlots in northern Rockingham County, Virginia. Two woodlots were mature oak-hickory stands; the other two were composed of brushy second growth hardwoods with dense undergrowth. Trap-mark-release procedures were conducted on the grids using 6-day trapping periods at 50-day intervals from July, 1972, through November, 1973. Excluding the winter catch, 415 individuals (285 *P. leucopus*) were examined for sex, age, reproductive condition and botfly larvae. Animals were marked with ear tags and by toe-clipping, and were released immediately. Age was determined by pelage. Small gray individuals and nearly adult mice in obvious postjuvenile molt were pooled as postjuveniles. Few of the former were caught, and thus this class was composed largely of mice 35 to 70 days old.[14]

Supplementary trapping was initiated to obtain bots for rearing, to sample other habitats, and to increase the overall sample size. During the summers of 1972, 1973, and 1974, removal traplines were established on nearby fields, fencerows, and woodlots, and also at higher elevations on Massanutten and Shenandoah Mountains. The sampled area was approximately 2000 km^2 and covered parts of Rockingham, Shenandoah, and Augusta Counties, Virginia. Traplines consisted of 30 traps at 15 m spacing, and were tended for three nights at a locality. Each sample was from homogeneous habitat. Sixty-five samples were taken from five kinds of habitats (Table 1), and 617 small mammals (366 *P. leucopus*) were removed. Total sample size from the two sources during bot seasons was 1032 mammals, including 651 *P. leucopus* (Table 2).

The large sample size of *P. leucopus* (651) facilitated statistical analysis of several facets of botfly infestation. Prevalence and burden by age and sex were compared using the RxC test of independence with the G-test.[23] Each paired class was compared using the G-test with 2x2 contingency tables.[23]

During July and August, 1973, 14 third instar larvae were obtained from trap-killed woodmice. In August, 1974, eight larvae were obtained after they dropped from cage live woodmice. All bots were placed in containers of moist sand to pupate. Puparia were then removed to small jars containing moist filter paper, where they remained until emergence.

RESULTS

Only one adult was reared from the 1973 batch, probably because all larvae were extracted prematurely from dead mice. Six adults emerged from the 1974 batch. All adults were identified as *Cuterebra fontinella* Clark. At room temperature (16-23 C.) and humidity (undetermined), pupation times for four flies averaged 52 days (range 46-71). Three others entered diapause and emerged after 198, 227, and 314 days.

Warbles were common in woodmice from late June through late October in all three years (Tables 2, 3). The earliest observation was on 29 May 1973, but no other bots were seen prior to 20 June in any year. Infestation probably continues into November or later, although none were collected in the smaller (<50) winter samples. Over the three seasons 199 (30.6%) of 651 *P. leucopus* were infested at least once (Table 2). In all years August was the month of peak prevalence (mean 42.2%).

TABLE 1. Prevalence of botfly infestation in woodmice from five different habitats. Pooled data represent 65 samples, each from homogeneous habitat.

Habitat sampled	No. mice examined	No. mice infested	Prevalence (%)	Mean burden
Mature forests	240	79	32.9	1.21
Second growth	259	116	44.8	1.32
Fencerows	68	3	4.4	1.33
Old fields	76	1	1.3	1.00
Pasture	8	0	0.0	0.00

TABLE 2. Monthly and annual bot prevalence in woodmice, 1972-1974. Winter results are excluded. Numbers in parentheses indicate sample sizes.

Year	Month							Total	Prevalence (%)
	May	June	July	Aug.	Sept.	Oct.	Nov.		
1972	—	—	6(19)	24(56)	7(42)	3(21)	—	40(138)	29.0
1973	1(32)	4(52)	—	28(54)	8(13)	9(44)	0(20)	50(214)	23.4
1974	0(12)	3(20)	10(26)	96(241)	—	—	—	109(299)	36.5
Total	1(44)	7(71)	16(45)	148(351)	15(55)	12(65)	0(20)	199(651)	30.6
Prevalence (%)	2.3	9.9	35.6	42.2	27.3	18.5	0.0	30.6	—

TABLE 3. Monthly observed parasite burdens, with data pooled from 1972-1974 bot seasons.

No. bots per host	Month							Total
	May	June	July	Aug.	Sept.	Oct.	Nov.	
0	43	64	29	203	40	53	20	452
1	1	6	13	114	10	9	0	153
2	0	1	3	31	4	3	0	42
3	0	0	0	1	1	0	0	2
4+	0	0	0	2	0	0	0	2
Total larvae	1	8	19	189	21	15	0	253
Mean burden	1.00	1.14	1.19	1.29	1.40	1.25	0.00	1.27

Across forested and brushy habitat bot infestation was general in woodmice (Table 1). Bots occurred in 32 of 34 August samples from wooded areas, and they were found at all elevations sampled from 330 m to 1300 m. Infestation was negligible in non-wooded areas, with bots in only two of 21 August samples. In pooled samples overall prevalence was 39.3% on wooded areas, compared to 2.6% in open habitat ($G = 98.76$, $P<0.001$). Within the pooled "wooded" class, prevalence was 44.8% in brushy second growth areas and 32.9% in mature hardwood forests ($G=7.41$, $P<0.01$). Demographic analysis of rodent populations on the woodlot grids (in manuscript) indicated that host densities in brushy areas and in mature forests were not significantly different. Density was not determined on the removal lines, but trap-night success and qualitative observations indicated that woodmice were only slightly less abundant in old fields and fencerows than in woodlots. Therefore bot prevalence does not appear to be a simple function of host density. The larger number of mice taken from wooded areas (77%) simply reflects the intensity of sampling.

Parasite prevalence was not independent of sex and age (RxC: $G_{3df}=15.21$, $P<0.001$) (Table 4). Bots occurred in 126 of 345 males, but only 73 of 306 females ($G=12.39$, $P<0.001$). Among postjuveniles 124 of 368 harbored bots, whereas only 75 of 283 adults were infested ($G=16.07$, $P<0.001$). Significant differences in prevalence were not found between postjuvenile and adult males ($P>0.10$) or between females ($P>0.10$). Adult males had a higher prevalence than adult females ($G=5.08$), $P<0.05$), and the same was true for younger males and females ($G=6.35$, $P<0.02$). The greatest overall prevalence occurred in postjuvenile males (39.1%).

TABLE 4. Bot prevalence in woodmice by sex and age, with data pooled from 1972-1974 bot seasons.

	Adult		Postjuvenile	
	Male	Female	Male	Female
Uninfested	91	117	128	116
Infested	44	31	82	42
Total	135	148	210	158
Prevalence (%)	32.6	20.6	39.1	26.6

Most warbles (98%) occurred at inguinal sites. Thus, most infested males had displaced testes. In five of six caged males, testes descended normally within 18 days after bots emerged. Heavy scar tissue prevented descent in the sixth. The effects of infestation on female reproductive organs are more difficult to evaluate. Data (in manuscript) show an upsurge of breeding activity among woodmice in August of 1972 and 1973, indicated by capture of many pregnant mice and by the presence of numerous small grey individuals in early fall. Thus the onset of fall breeding in woodmice in Virginia occurs at the time of peak botfly infestation. On the woodlot grids, 57 mature females were captured during August trapping periods. Of 20 infested mature females, only two were lactating or obviously pregnant. Among healthy females, 28 of 37 were obviously in reproductive condition. Apparently, fitness in individual hosts and reproductive value in host populations are altered by temporary sterility, mechanical blockage, or other physical or behavioral changes in infested mice.

Obvious parasite burden did not vary appreciably from 1.2 bots per infested mouse during the bot season (Tables 1, 3). Since mice were not skinned in search of early instar larvae, the true mean burden was probably somewhat higher. Burden was independent of sex and age ($P>0.05$), and was not significantly higher in brushy habitat than in mature forests ($P>0.05$). Nearly 23% of the infested woodmice were multi-infested. Of 199 infested mice, 77% had one bot, 21% harbored two, 1% carried three, and 1% had four or more. One mouse with six visible warbles died in the laboratory during larval emergence. Although this was the only mouse known to have succumbed directly to bots, all multi-infested animals were debilitated. Infested mice were more subject to trap-induced shock (nearly 15% were found dead in Sherman traps) and they remained disoriented longer following release at the trap site.

Thirteen other species of mammals (381 individuals) were examined for bots and emergence scars. Unidentified bots were recorded from one of 34 *P. maniculatus nubiterrae*, three of 25 *Tamias striatus*, and three of 52 *Microtus pennsylvanicus*. Adult flies were not reared from larvae infesting deermice and voles. However, these two species, where infested, were sympatric with infested woodmouse populations. Bots were inguinal in the deermice, but were on the neck or sides in voles. The chipmunk bots were another species, tentatively identified as *C. emasculator* Fitch. Botfly larvae were absent in 24 *P. maniculatus bairdii*, eight *M. pinetorum*, three *Clethrionomys gapperi*, two *Zapus hudsonius*, one *Reithrodontomys humulis*, 17 *Mus musculus*, four juvenile *Sciurus carolinensis*, two *Tamiasciurus hudsonicus*, 122 *Blarina brevicauda*, and 87 *Sorex* spp.

DISCUSSION

Botfly larvae in rodents seem to have infective seasons which vary according to climate. The duration of the season in this study (June to November) was similar to bot seasons for rodents reported from southern Michigan[23] and British Columbia,[12] slightly shorter than those in Missouri[3] and Tennessee,[8] and considerably longer than those in Ontario[20] and the northern United States.[9,16,17] These reports involve several species of flies and rodents, but a pattern of climatic influence is apparent.

The principal host for *C. fontinella* in upland Virginia seems to be *P. leucopus*. This is apparently true in other regions as well.[8,23,24] The woodmouse occurs in nearly every conceivable habitat in Virginia. At elevations above 850 m it is sympatric with *P. maniculatus nubiterrae*. Along cultivated highway property and in old fields it occurs with *P. maniculatus bairdii*. Warbles were always negligible or absent in the two deermouse subspecies, even where they were more abundant than heavily infested woodmice. Similar findings were reported for sympatric, congeneric *Peromyscus* populations in Michigan.[24] The usual species infesting the deermouse in the western United

States is *C. grisea*.[12] This species is taxonomically close to *C. fontinella*, and intermediates between the two have been found where both are present.[11] This evidence prompts speculation about recent speciation in the Cuterebridae and progressive adaptation in related host taxa of mechanisms to prevent or abort infection. Both hosts and parasites are easily obtained, and would be excellent subjects for research on host-parasite coevolution or niche divergence in the genus *Peromyscus*.

The overall prevalence of infestation (30.6%), parasite burden (1.27), and site selection (98% inguinal) are in general agreement with most other reports.[8,12,16,20,22] However, other reports of prevalence by sex and age have been highly variable and often contradictory. Some have reported highest prevalence in males,[12,20] highest in females,[7] highest in adults,[12,17] or no correlation by sex or age.[8,23] In this study postjuvenile males were the class most often infested in all three years. However, in this study the postjuvenile class included animals in the postjuvenile molt. Most other researchers assigned age classes by weight, and therefore most such molting mice were labeled as adults. Significantly, this age group (35 to 70 days old[14]) seems to bear the brunt of infestation. Many such mice are in the process of establishing territories. Their searching behavior probably causes additional contact with infective larvae, and this could easily account for the higher prevalence of parasitism. Another possible explanation for higher prevalence in postjuveniles is natural or acquired immunity in a percentage of mice. If immunity is acquired, it is not general, because many mice in this study were infested repeatedly in subsequent recaptures. However, data are insufficient to preclude the possibility of incomplete immunity.

Although the observed dearth of bots in field populations of rodents is in agreement with other reports,[1,8,9,17] the general nature of infestation over a large region is not so well supported. Others often have reported localized islands of heavy infestation surrounded by seemingly favorable habitat with dense host populations but few or no bots.[8,9] Bots were found in 95% of the samples from wooded areas in the present study. One explanation is that potential aggregation sites may have been more localized in some of these reports. Reported aggregation behavior in other *Cuterebra* indicates that flies gather for mating at sunny locations near topographic summits (hillside, tall tree), after which gravid females seek out the hosts' habitat to deposit eggs on debris and vegetation.[6,11] Assuming that *C. fontinella* behaves similarly, infestation should be limited more by a lack of potential aggregation sites than by open habitat, as long as a sufficient host population is present. Support for this has been seen in the *C. buccata*—cottontail relationship (H. Jacobson, personal communication), where prevalence by habitat is the reverse of that seen in the rodent bots of the present study. Old field cottontails were much more heavily infested than those in woods or brush. With this in mind, I predict a high and general prevalence of *C. fontinella* in woodmice from second growth woodlands on hilly or boulder-strewn terrain. Such areas have a combination of topographic summits, many sunny exposures, and available host habitat. In such environments, typical throughout the Central Appalachians, botfly parasitism in woodmice seems to be a general phenomenon.

Available evidence indicates that bot-caused mortality is trivial,[8,17] but that secondary mortality may be considerable, whether due to bacterial infection[2] or possible increased vulnerability to predation.[2,17,23] Of greater long-term consequence is the possibility of sterility, whether temporary or permanent, due to inguinal encapsulation sites or other causes. In this study most infested mice seemed to be disassociated from the reproductive pool during a major part of the fall breeding season. The long-term effects of temporary sterility in part of a population are unknown and merit further study. Apparently, botflies exert an effect on both natality and mortality rates in *P. leucopus*. Obviously, the effect of lowering natality while raising mortality should be to damp population fluctuations, although there is no firm evidence that this is happening. It is intriguing to suggest that this host-parasite relationship could be partly responsible for the inordinate stability of *Peromyscus* populations in many regions. To measure these effects and answer evolutionary questions we need additional quantified data on prevalence of bots on all normal hosts, supplemented by biodemographic analyses of infested host populations.

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