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Source: Journal of Wildlife Diseases, 14(1) : 56-66

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-14.1.56

BOT FLY MYIASIS OF THE COTTONTAIL RABBIT, *Sylvilagus floridanus mallurus* IN VIRGINIA WITH SOME BIOLOGY OF THE PARASITE, *Cuterebra buccata*

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Abstract: Twenty four percent of 2,643 cottontail rabbits *(Sylvilagus floridanus)* collected in Virginia from 1949-1975 showed evidence of *Cuterebra* parasitism. Occurrence was seasonal with greatest prevalence from July to November. Some *Oryctolagus cuniculus, S. palustris* and one *S. transitionalis* also showed *Cuterebra* myiasis. Juvenile rabbits had higher infection rates (28%) than did adult rabbits (14.5%, $P < .001$). Juveniles had greater numbers of larvae per host than adults, with means of 2.14 and 1.62, respectively. Larval development sites were in the genital region of most hosts. Twenty flies reared from wild cottontails were identified as *C. buccata*. Duration of induced infections in *Oryctalagus* was 30-33 days. Minimal generation time for *C. buccata* is concluded to be 11 weeks, allowing up to four generations of flies to occur annually in the southern and one generation to occur in the northern distributional limits of this bot fly. *Peromyscus* hosts were refractory to *C. buccata* infections. *C. buccata* fecundity averaged 1316 eggs. Field observations of adult flies are described.

INTRODUCTION

Bot flies in the genus *Cuterebra* (Diptera, Cuterebridae) are obligate, myiasis-producing parasites associated most often with lagomorphs and rodents in North America. Documented host responses to *Cuterebra* infection include anemia, [8,13,34] changes in leukocyte count, [8,13,17] plasma protein alternation, [26] splenomegaly and lymph node enlargement, [13] lowered body weight, [3,17] lowered reproductive efficiency [34] and lowered bone marrow fat content. [27] Changes in host activity [8] and host mortality [3,8,11,17,28] also have been reported. Mortality due to secondary causes such as susceptibility to predation, [8,33,34] screwworm infection [24] and bacterial infection [7] have been suggested.

These parasites have a major impact on the consumption and recreational use of small game. Thousands of small game mammals are discarded annually by hunters who erroneously believe that bot larvae or their lesions make game inedible. [1]

Pathologic effects of this parasitism are greater in abnormal or non-native hosts. In these cases, larval migration tends to be erratic and the larval development site on the host is likely to be accompanied by greater than normal inflammation. Abnormal hosts in which *Cuterebra* have been reported include man, dog, fox, cat, cattle, hog, deer, skunk, shrew, oppossum and

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woodcock.[2,14,20,21,32,37] Rabbit bot fly larvae, identified by single-pointed body spines[3] most often are the cause of these incidental infections.

Cottontail rabbits (*Sylvilagus* spp.) are the normal hosts of four *Cuterebra* species; *C. buccata, C. cuniculi, C. lepivora* and *C. abdominalis*. The last species is the valid synonym for *C. horripilum*.[31] In addition, Baird[3,4] found cottontail rabbits to be suitable hosts for *C. jellisoni* and *C. ruficrus* which have jack rabbits (*Lepus* spp.) as normal hosts.

This paper reports the prevalance of *Cuterebra* parasitism in wild populations of cottontail rabbits in Virginia and describes laboratory and field observations on the life history of *C. buccata*, a widely distributed species parasitizing *Sylvilagus floridanus mallurus*, the eastern cottontail rabbit. The large fly (18-20mm in length) is black and white and has red eye spots. Its geographic range extends from Minnesota to Texas and from Nova Scotia to Florida.[36] However, Haas and Dicke[19] found it to be relatively rare in its northern range.

MATERIALS AND METHODS

Observations recording the prevalence of *Cuterebra* myiasis of cottontail rabbits were made by members of the Virginia Cooperative Wildlife Research Unit from 1949-1975. A total of 2,643 rabbits was sampled by trapping or shooting and examined for signs of *Cuterebra* parasitism. Host sex was recorded for 1,251 rabbits and age, determined by eye lens weight,[30] was recorded for 665 rabbits. The locations of larval development sites were recorded for 460 larvae on wild and laboratory hosts. Although continuous collection of rabbits from any one geographic location and in any one year was not possible, a composite record of prevalence on a monthly basis was compiled from 995 rabbits for which the month of collection was known.

Adult flies were reared in the laboratory, either from late third stage larvae collected from wild hosts, or from induced infections in laboratory rabbits, *Oryctolagus cuniculus*. Field collection sites of late stage larvae were in Nottoway Co. and Montgomery Co. in the Piedmont and Mountain regions of Virginia, respectively. Infective larvae were hatched from eggs obtained either from reared or wild caught female bot flies. For reared flies, mating was induced using tethering techniques[10] and laboratory infections were made following the general procedures described by Baird.[3] Infections of laboratory rabbits were made with five larvae per host introduced in oral or nasal portals. Rabbit hosts were restrained until positive entry was affected by the larvae.

Egg counts were made from dissected reared or captured females. Dried, pinned specimens were softened and hydrated before dissection in warm water containing a small amount of wetting agent (e.g. trisodium phosphate). Puparia were placed in damp peat moss and kept at room temperature (circa 23 C) prior to adult emergence.

Field occurrence data of adult *C. buccata* were taken from pinned specimens in the following reference collections: American Museum of Natural History (New York City); Auburn University (Alabama); Bishop Museum (Hawaii); Brooks Museum, University of Virginia (Richmond); California Insect Survey (Berkeley); Clemson University (South Carolina); Cornell University (Ithaca, New York); Florida State Agriculture Collection (Gainesville); Indiana University (Bloomington); Kansas State University (Manhattan); Michigan State University (East Lansing); Museum of Comparative Zoology, Harvard (Cambridge); National Resources Laboratory (LaVale, Maryland); North

Carolina State University (Raleigh); Ohio State University (Columbus); Philadelphia Academy of Science, R. Painter Collection (Manhattan); Texas A and I University (Kingsville); Texas A and M University (College Station); University of Arkansas (Fayetteville); University of California (Riverside); University of Delaware (Newark); University of Georgia (Athens); University of Kansas (Lawrence); University of Nebraska (Lincoln); University of Northern Iowa (Cedar Falls); University of Wisconsin (Madison); and U.S. National Museum (Washington, D.C.). Field observations of adult flies were made in Delaware.

The binomial procedure[16] was used for statistical analysis of the data.

RESULTS

Cuterebra myiasis in Virginia

Bot fly myiasis of the eastern cottontail rabbit was widely distributed in Virginia, ranging from coastline to mountains. Infections of *S. palustris,* the marsh rabbit, were found on Hog Island in Surry County. Infections in domestic rabbits *(O. cuniculus),* which were permitted to roam freely in backyards and surrounding fields, were reported from Stafford and Chester Counties. One New England cottontail rabbit *(S. transitionalis)* was infected with *Cuterebra* in Giles County (W. M. Murphy, pers. comm.).

With the exception of the New England cottontail, all reports occurred in localities characterized by, or in close association with, old field habitat. The New England cottontail was captured in an area consisting of a large expanse of hardwood forest at high elevation.

Of 2,643 eastern cottontail rabbits examined for *Cuterebra* myiasis from 1949-1975 in Virginia, 24% were found either to be infected by *Cuterebra* or to have larval emergence scars as evidence of recent infection. The occurrence of this myiasis was seasonal. The composite prevalence on a monthly basis for nearly 1,000 eastern cottontail rabbits in Virginia is given in Figure 1. Prevalence of over 20% occurred for five consecutive months beginning in July. The overall prevalence for the 895 rabbits examined during the eight months of observed infections was 22%. No significant differences ($P < 0.05$) were found between the prevalence of infection of male and female rabbits, but juvenile rabbits had significantly ($P < 0.001$) greater prevalence of infection and number of larvae per host (Table 1). The maximal number of larvae on any one host was nine. The most common area of larval development was the genital region followed by side and shoulder regions for infections of wild rabbits (Table 2). Comparative prevalence of *Cuterebra* myiasis during different years from the same localities and at different host densities is given in Table 3. Host density is inferred from ratios of rabbits taken to trapping and hunting efforts expended. No trends are apparent.

Biology of *C. buccata*

The seasonal occurrence of 106 field captured adult flies recorded from museum specimen labels is plotted by geographic latitude in Figure 2. Also plotted are the dates of collection of mature larvae from 23 *Sylvilagus* hosts and approximated flight dates for 23 unseen adult flies which laid eggs that produced these larvae. Because the combined egg and larval development time of 6 weeks is relatively constant, the flight dates for unseen flies can be approximated by subtracting development time from the date of mature larval drop. The approximated date is the latest that the parental fly could have been active and does not account for unhatched egg survival for periods beyond egg development time. The solid lines in Figure 2 give the probable

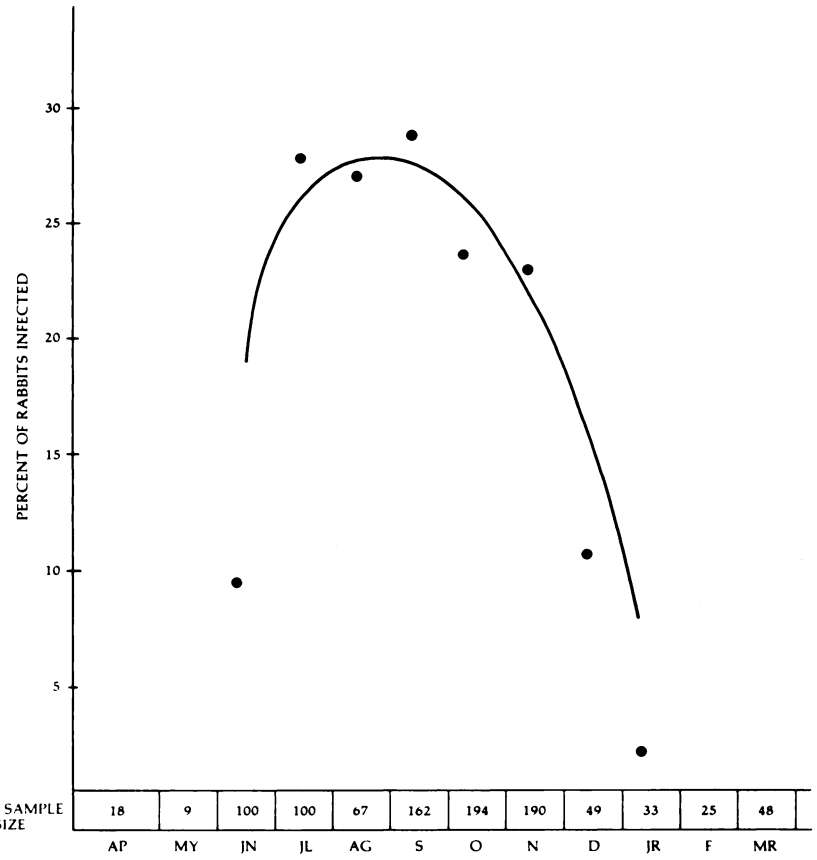

FIGURE 1. Monthly percent occurrence of *Cuterebra* myiasis on *Sylvilagus floridanus* in Virginia (1949-1975).

TABLE 1. Prevalence of *Cuterebra* parasitism by host age and sex in wild *Sylvilagus floridanus* collected in Virginia.

	Rabbit Age Class [a]		Rabbit Sex [b]	
	Juvenile	Adult	Male	Female
Number of Rabbits	307.00	358.00	649.00	602.00
Percent Infected	28.00	14.50	28.80	30.10
Mean Number of Larvae Per Infected Host	2.14	1.62		

[a] Age classes are significantly different in infection prevalence at $P < 0.001$ ($X^2 = 17.8$, ld.f.)

[b] No significant differences between sexes at $P < 0.05$ ($X^2 = 0.25$, ld.f.)

TABLE 2. Percent occurrence of developing *Cuterebra* larva at different sites on wild *(Sylvilagus floridanus)* and laboratory *(Oryctolagus cuniculus)* rabbit hosts.

Development Site On Host	*O. cuniculus* (20 larvae)	*S. floridanus* (440 larvae)
Genital	65.0	46.4
Belly, rib cage or shoulder	20.0	36.1
Neck or face	0.0	8.6
Back	10.0	8.2
Other areas	5.0	0.7

TABLE 3. Index of cottontail rabbit *(Sylvilagus floridanus)* population density and prevalence of *Cuterebra* myiasis in two Virginia localities, 1960-61 and 1973-74.

		Incidence of Cuterebra Myiasis [a]		Host Population Index [b]	
Locality	Year	Number of Rabbits Collected	Percent Infection	Trap Nights Per Rabbit Captured	Man/Days Hunting Per Rabbit Killed
Fort Pickett Nottoway Co.	1960	27	41	22.2	4.4
"	1961	10	10	83.0	7.2
"	1973	18	78	191.0	16.2
"	1974	18	33	c	65.6
Radford Montgomery Co.	1973	18	50	56.0	d
"	1974	20	10	68.4	d

[a] Only includes data from rabbits collected during the month of September.

[b] Trap nights per rabbit capture were only recorded during September; however, rabbit kill figures were collected at a game-check station for the entire hunting season.

[c] No trapping was attempted; rabbits were collected by shooting.

[d] No hunting was allowed at this locality.

seasonal limits for *C. buccata* adults in its north-south distribution in the United States.

Adult emergence dates for 20 flies reared from larvae collected from eastern cottontail rabbit hosts ranged from 11 February to 13 October. Adult emergence dates for nine flies reared from induced infections of laboratory rabbits ranged from 10 March to 4 December. The sex ratio for reared flies favored females; for flies reared from eastern cottontail rabbits, it was 1:2 and from laboratory rabbits 1:5.

Longevity of reared flies averaged seven days (range 3-10 days) and two wild caught female flies each lived five days beyond their capture date. Spontaneous oviposition began three days after eclosion for flies held at 25 C.

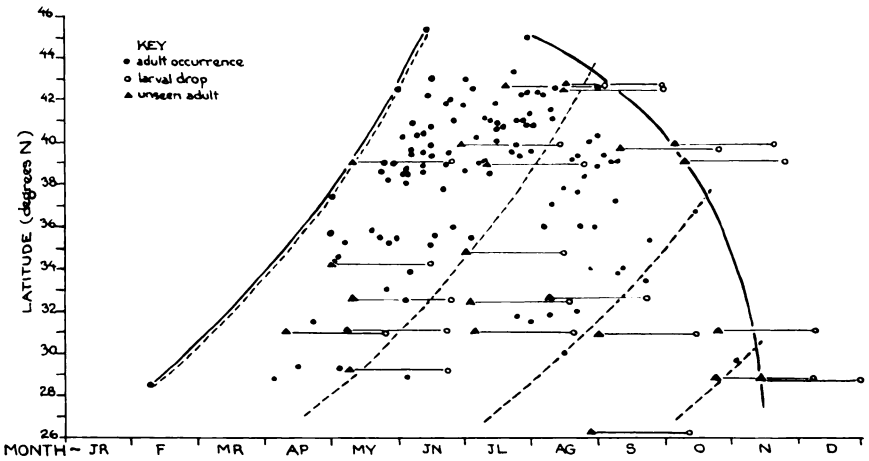

FIGURE 2. Seasonal occurrence of *Cuterebra buccata* by geographic latitude as recorded on hand caught adult specimens and mature larvae in *Sylvilagus* hosts (1906-1977) (heavy solid lines estimate seasonal limits; dotted lines, based on a minimal generation time of eleven weeks, estimate possible adult flight seasons).

Egg counts for six flies ranged from 1017 to 1591 (mean 1316). Three females reared from larvae removed from free-ranging eastern cottontail rabbits averaged 1534 eggs; whereas for three flies produced from induced infections of laboratory rabbits, the average was only 1098. Most eggs held at 25 C hatched in response to warming stimulus (human breath) after seven days.

The earliest signs of infection in hosts were seen 10 days after infection. In laboratory rabbits, adverse signs of infection in the form of audible wheezing, sneezing and temporary paralysis of the hind limb occurred in a few hosts 10 days following introduction of larvae. Larval breathing sites were first seen as skin lesions on laboratory rabbit hosts 10 days post infection. Moulting from second to third stage larvae occurred on about the seventeenth day post infection. Larval development sites on *O. cuniculus* also are shown in Table 2. Note that over 80% of the laboratory-induced infections with *C. buccata* and a similar proportion of wild *Cuterebra* infections developed at genital, belly, side or shoulder sites. Larvae (12) dropped from laboratory rabbit hosts from 30 to 33 days after infection. Pupation occurred within 48 h. after larvae left their hosts. The shortest pupation period recorded was 34 days. This male specimen developed from a mature larva removed from a dead eastern cottontail rabbit early in July. All other flies entered diapause and emerged from puparia in the spring even though they were held at about 25 C during the winter months. From these data, the minimal generation time for *C. buccata* is estimated at 77 days or 11 weeks.

All laboratory rabbits challenged with infective larvae became infected, but only 44% of the introduced larvae developed beyond Larva II. About one half of these larvae completed development and pupated and about one half of these emerged later as adults. Thus 12% of the initial infective dose developed to adults. Attempts to infect five *Peromyscus leucopus* with a dosage level of three larvae per host were unsuccessful.

Field behavior of adult *C. buccata* was observed six times. These observations involved both sexes, but not coincidentally. Males were seen twice in midmorning (circa 1000 h.) perched on exposed branches and leaves of vegetation growing on the inland side of beach sand dunes near Rehobeth, Delaware. The males appeared to make pursuit flights of other passing insects. Both days were overcast.

Female *C. buccata* were seen on four occasions. The hour of day was between 1000-1100 and air temperatures between 25 and 28 C in all instances. All appeared to be searching for oviposition sites, or hosts, along established rabbit runs or wheel tracks at the edge of woodland bordering salt marsh. These individual flies flew slowly at less than 30 cm above the ground in an erratic searching pattern. From time to time they alighted on vegetation overhanging the path. Movement by the observer appeared to startle the flies and they would fly off at great speed. Careful examination of vegetation on which these flies had alighted failed to produce any eggs.

DISCUSSION

Seasonal occurrence of adult *C. buccata*

North of 38°N latitude the occurrence of adult *C. buccata* is concentrated from June through August. Records from more southern latitudes show adults to occur from early April into October. The weak clustering of points in southern latitudes in Figure 2 suggests two flight seasons: one from April through mid-June and the other from mid-July through September. More synchronous occurrence of adults into distinct flight seasons, in southern areas at least, seems advantageous in view of the short reproductive life span of these flies.

With an approximate minimal generation time of 11 weeks, the number of annual larval seasons possible for *C. buccata* ranges from four in the deep south to one in the north (Fig. 2). This agrees with the conclusions of Farlow *et al.*[15] for *Cuterebra* infections in eastern cottontail rabbits in Louisiana. This also is supported by prevalence of *Cuterebra* recorded for eastern cottontail rabbits in Virginia where flight seasons probably occur in May and August (Fig. 2) to produce midsummer infections plotted in Figure 1.

Larval site specificity

Site specificity for larval development is documented for several *Cuterebra* species.[3,4,11,12] The site location for development of *C. buccata* appears to be genital, belly and rib-cage regions in decreasing order. Baird[3,4] reported host partitioning by *C. jellisoni* and *C. ruficrus* in *L. californicus*. Hass and Dicke[19] found *C. abdominalis* developing primarily on the neck of eastern cottontail rabbits in Wisconsin. They considered *C. buccata* to be rare. Boisvenue[9] concluded that *C. buccata* occurred in mixed infections with *C. abdominalis* in Michigan. However, nearly all of the infections he found were in the neck region of cottontail rabbits, indicating that *C. abdominalis* predominated. The low percent of warbles on neck and head sites of eastern cottontail rabbits in Virginia suggest that *C. abdominalis* was encountered only rarely.

Host age and *Cuterebra* prevalence

Within the limits of the indices (trapping and man/days hunting success) used to estimate host density in Virginia, there is no consistent indication that *Cuterebra* infections are proportionate to host density or are density dependent. However, it is still likely that parasitism by *C. buccata* is related to host density. Two factors could be responsible for the lack of apparent density relationships seen in these data (Table 3). Environmental conditions at the site may have an

equal or greater effect on prevalence of host infection than host density. Inclement meterologic conditions might greatly alter survival of eggs, adult flies and pupae. Additionally, changes in host population age structures could have major effects on incidence of parasite infection. Because juvenile rabbits have a higher prevalence of infection and carry more larvae than adults (Table 1), we infer that prevalence will be highly dependent on host natality and on the survival of juvenile segments of the host population. Juvenile recruitment rates can be highly variable at different periods of the host's breeding season. For example, poor survival of the first cottontail rabbit litters of the year could result in low parasite abundance during the second and third flight seasons. Host populations could still reach high density, if population recruitment of juvenile rabbits during the remainder of the breeding season was high. Obviously, the reverse situation also could occur.

There are two factors which could account for greater parasitism of juvenile rabbits than adults. Exploratory behavior of young animals pioneering from maternal nest areas could subject juveniles to greater risk of exposure to unhatched *Cuterebra* eggs. This also has been suggested as the reason for higher levels of bot fly infections in young woodrat and chipmunk hosts.[8,12] The probability that older hosts acquire immunity to *Cuterebra* infections also may help account for higher infection rates in juveniles. Immune reactions have been demonstrated in laboratory rabbits infected with *C. buccata*[38,39] and high blood serum globulin levels have been demonstrated in *Cuterebra* infected eastern cottontail rabbits,[23] which supports an immunity hypothesis. Hensly[22] suggested that white footed mice *(P. leucopus)* may acquire partial immunity to *C. fontinella* myiasis. Recent studies by Gingrich and Barrett[18] have demonstrated the development of immunity in *Peromyscus* following repeated *Cuterebra* infections.

Development of *C. buccata* in rabbit hosts

Comparative timing of events in the larval developments of *C. buccata* in eastern cottontail rabbit and laboratory rabbit hosts has not been done. Superficially, from fragmentary field data, such events as initial appearance of the larval breathing pore, duration of developing stages and time of larval drop appear similar in these different hosts. These events in induced infections of laboratory rabbits also closely match the timing reported for *C. jellisoni* in several lagomorph hosts.[3] Note that *C. ruficrus* is a slower developing species in all hosts and thus is not comparable.[4]

Adult biology of *C. buccata:*

Longevity of flies reared here matched that reported for other *Cuterebra* species.[3,12,35] The egg capacity for *C. buccata* reared from eastern cottontail rabbit hosts was intermediate between those of *C. jellisoni* and *C. ruficrus*.[3,4] However, lower egg counts for *C. buccata* developing in laboratory rabbits suggests a lower fecundity resulting from parasitism of a non-native host.

Although the data are scant, there appeared to be a differential sex ratio favoring female flies. This may be an experimental artifact resulting from differential pupal survival of sexes under laboratory conditions, or it may be similar to the sex ratio differences reported by Smith[35] for *C. approximata* in two species of *Peromyscus*. Most workers have dealt only with the effects of myiasis on the host and not the concurrent effects on the parasite, unless the effects were immediately apparent. Such possible manifestation as parasite adult sex ratio, fecundity

and longevity as influenced by optimal and suboptimal hosts may be useful in clarifying distributional patterns and phylogenetic relationships of bot flies. The application of these differential responses to select resistant host traits or to treat myiasis biochemically could serve as part of an integrated myiasis control program by affecting long-term survival of the bot fly population.

Many aspects of the field biology of *C. buccata* remain unknown. The apparent native host, the eastern cottontail rabbit, is not easily trapped or maintained in a laboratory. In addition, the common occurrence of *Cuterebra* larvae in wild *Sylvilagus* populations contrasts sharply with the desultory observations of adult flies. Mating, resting and flight habits remain a mystery. The rather consistent occurrence of gravid females hovering and alighting in potential host habitat indicates that oviposition occurs in midmorning.[6,25,29] Perhaps, like *C. tenebrosa*,[5] other adult activity occurs in twilight when most observers are not afield.

Acknowledgements

We thank Charles L. Graham, USDA, ARS, Fredrick, Maryland and Curtis W. Sabrosky, U.S. National Museum, Washington, D.C. for their generosity and efforts in obtaining most of the specimen distribution records used in this study.

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Received for publication 5 April 1977