The Effect of Bot Fly Larvae on Reproduction in White-footed Mice, Peromyscus leucopus[1]

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ABSTRACT: The effect of bot fly larvae on reproduction in white-footed mice (*Peromyscus leucopus noveboracensis*) was determined from a sample of 1050 mice that were snap-trapped over a 2-year period in E-central Minnesota. Bot fly larvae (*Cuterebra fontinella* Clark, 1827) were found parasitizing mice from 16 July through 2 October. During July, August and September, 9.2% of the mice trapped were parasitized by *C. fontinella;* the mean infestation rate was 1.4 larvae per infested mouse. A single bot fly larva (or scar) was found on 69.1% of the parasitized mice; 23.7% of the mice carried two larvae; 6.2% carried three larvae, and 1.0% had four larvae. More male mice were trapped than females (56.3% - 43.7%) and, correspondingly, 55.4% of the bot fly larvae were found on male mice and 44.6% on females. Older mice were more heavily parasitized than younger mice. Parasitized subadult male mice had smaller testes, epididymides and seminal vesicles than nonparasitized subadult males. In adult male mice, the presence of one larva had little effect on the size of the reproductive organs. In adult female mice, parasitism by bot fly larvae did not cause a decrease in the number of embryos, corpora lutea or placental scars. Spleen size increased greatly when larvae were present. The hypothesis is presented that this host-parasite relationship is stable and that the host and parasite have evolved coadaptations and a tolerance for each other.

INTRODUCTION

The effect of bot fly parasitism on rodents has long been debated, but few concrete data exist. Scott and Snead (1942) suggested that white-footed mice [*Peromyscus leucopus* (Rafinesque)] parasitized by bot fly larvae were awkward and less efficient in escaping predators. It has been proposed that bot fly larvae interfere with reproduction in their host; Sillman (1955) observed that three female white-footed mice infested with larval cuterebrids were unable to rear litters successfully in the laboratory. Weights of the testes, ovaries and uteri were less in deer mice [*Peromyscus maniculatus* (Wagner)] artificially infected with larval cuterebrids than in noninfected controls (Smith, 1977). Early workers thought that larvae directly or indirectly castrated their male hosts (Dalmat, 1942; Seton, 1920, 1929). Wecker (1962) noted that, because of the presence of bot fly larvae, the testes of several adult male white-footed mice had not descended into the scrotum. Several authors have suggested a correlation between heavy larval infestations one year and low populations of mice the next year (Jameson, *in* Dalmat, 1943; Scott and Snead, 1942; Wecker, 1962; Wilson, 1945). Dalmat (1943) noted several instances of death in white-footed mice from unknown causes at the time larvae were emerging. Miller and Getz (1969) postulated that *Cuterebra* had no effect on reproduction in their hosts, but that infected mice had a lower survival rate than noninfected mice. In contrast, it also has been suggested that bot fly larvae do little, if any, damage to their hosts (Clough, 1965; Buckner, 1958; Test and Test, 1943).

Cuterebra larvae have been found to have a definite physiological effect on their hosts. Significantly lower erythrocyte counts, lower hematocrit percentages, lower albumin-globulin ratios, and lower hemoglobin concentrations were found in mice infested with cuterebrid larvae, while the leucocyte number, spleen size and thymus size were significantly larger (*see* Bennett, 1973; Childs and Cosgrove, 1966; Clough,

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1965; Dunaway *et al.,* 1967; McKinney and Christian, 1970; Payne *et al.,* 1965; Selander, 1961). Tissue damage by *Cuterebra* was reported by Payne and Cosgrove (1966), but they found healing and repair of damaged tissues to be rapid once the bot emerged. What these physiological changes actually mean to the infected mouse in terms of cost of fitness has not been ascertained.

The purpose of this article is to examine and quantify the effect of bot fly larvae, *Cuterebra fontinella* Clark, 1827, on reproduction in their primary host, *Peromyscus leucopus,* and to present the hypothesis that the parasite-host relationship is stable and that the host and the parasite have evolved coadaptations and a tolerance for each other.

METHODS

A total of 1050 white-footed mice [*Peromyscus leucopus noveboracensis* (Fisher, 1829)], were examined for bot fly larvae or scars indicating recent emergence of larvae. White-footed mice were captured at the Cedar Creek Natural History Area, Anoka and Isanti counties, and Carlos Avery Game Refuge, Anoka County, Minnesota, every 2 weeks from September 1956 through September 1958. Cedar Creek and Carlos Avery are located approximately 45 km N of Minneapolis and St. Paul in E-central Minnesota. The areas are characterized as mixed deciduous forest with open fields and are located on a broad expanse of glacial outwash sand known as the Anoka Sand Plain. Trapping for white-footed mice was conducted primarily in oak woodlands and to a lesser extent in maple-basswood stands. For details on vegetation, climate and soils of the study areas see Rand (1953), Pierce (1954), Ovington *et al.* (1963), Moore (1973) and Grigal *et al.* (1974).

Standard external measurements (total length, length of tail vertebrae, length of hind foot and height of ear from notch) and weight were recorded for all mice captured. On the basis of size and pelage, each mouse was placed into one of three age classes: juvenile, subadult or adult. For males the following reproductive data were recorded: (1) testes, length in mm (2); testes, abdominal or scrotal; (3) testes sperm present or no sperm; (4) epididymides, tubular or undeveloped; (5) epididymides, sperm present or no sperm, and (6) seminal vesicles, developed or undeveloped. The testes, epididymides and seminal vesicles were weighed to the nearest 0.1 μg. For females the following reproductive data were recorded: (1) ovary, number of mature follicles or corpora lutea left and right; (2) embryos, number left and right, and (3) placental scars, total number left and right. Additionally, the spleen of each mouse was weighed to the nearest 0.1 μg.

Several live white-footed mice infested with bot fly larvae were brought into the laboratory, the larvae allowed to pupate, and adult cuterebrids reared in order to determine the species of *Cuterebra* involved. Reference specimens of the bot flies are deposited in the entomology collection of the University of Minnesota, St. Paul.

Primary host is defined here as the host species in which the parasite is most often found, and also that host in which the parasite appears most successful in completing its life cycle.

RESULTS

Cuterebra fontinella Clark, 1827 (=*C. angustifrons* Dalmat, 1942, *see* Sabrosky, 1972) was the only species of bot fly found to be parasitizing white-footed mice. For the months of July, August and September, the mean infestation rate was 1.4 larvae per infected mouse; 9.2% of the white-footed mice trapped during these months were parasitized by cuterebrids. Of the 97 mice found to be infested with cuterebrids, 67 (69.1%) carried a single bot fly larva or the scar from a recently emerged larva, 23 mice (23.7%) had two larvae, six mice (6.2%) had three larvae, and a single mouse (1.0%) had four larvae. Larval *C. fontinella* were found on white-footed mice from 16 July through 2 October; scars from single, recently emerged larvae were observed on mice captured between 12 August and 23 September.

Males comprised 56.3% and females 43.7% of the white-footed mice captured. Correspondingly, 55.4% of the bots were found in male mice and 44.6% in females. These results were not significantly different as tested by chi-square. This close correlation suggests that the newly hatched bot fly larva does not preferentially select a mouse of one sex over one of the other, but attaches itself to the first mouse it encounters. The larger percentage of male mice either reflects a greater percentage of males in the population or indicates that males were more mobile than females and hence more likely to be trapped or to encounter a cuterebrid egg.

Older mice were proportionally more heavily parasitized than younger mice. Mice classified as adults (34.8% of the population) had 51.0% of the bot fly larvae, subadults (45.9% of the population) had 30.2%, and juveniles (19.3% of the population) had 18.8%. These frequencies were tested with chi-square ($X^2 = 13.7$) and found to be significant at the .001 level of confidence. Thus, bot fly larvae were not distributed randomly throughout the mouse population; subadult and adult white-footed mice were more heavily infested with bots than were juveniles.

In subadult male mice, the length of testes and the weights of the testes, epididymides and seminal vesicles were significantly less in mice carrying cuterebrids (Table 1). Descent of testes, sperm in the testes, development of epididymides, sperm in the epididymides and development of the seminal vesicles were not significantly different in parasitized vs. nonparasitized mice although the mean values were smaller for infected mice.

In adult male white-footed mice, the presence of one bot seemed to have little effect on the mouse. The testes, seminal vesicles and epididymides were similar in both parasitized and nonparasitized adult male mice. However, the presence of two or more cuterebrids resulted in a trend toward smaller testes and epididymides, but the differences compared to mice not carrying cuterebrids were not statistically significant.

For adult female white-footed mice there was no significant difference in the number of embryos, corpora lutea or placental scars between mice infected with bot fly larvae and those not infected by bots (Table 2). Although sample sizes were small, the trend is actually opposite to the direction predicted; parasitized mice tended to

TABLE 1.—Reproductive characteristics (means ± SE) of subadult male white-footed mice with and without *Cuterebra* larvae. Lengths are in mm and weights in μg. All p values derived from t-test

	With *Cuterebra* (N = 18)	Without *Cuterebra* (N = 286)	
Testes length	4.7 ± .35	5.7 ± .15	$p<.05$
Testes weight	219.2 ± 77.3	520.3 ± 39.8	$p<.001$
Epididymis weight	30.8 ± 9.2	51.4 ± 3.9	$p<.05$
Seminal vesicle weight	108.8 ± 62.1	330.9 ± 40.8	$p<.001$

TABLE 2.—Reproductive characteristics (means, N, and SE) of adult female white-footed mice with and without *Cuterebra* larvae

	With *Cuterebra*	Without *Cuterebra*
Active corpora lutea	5.6(14) ± .66	4.8(83) ± .17
Embryos in uterus	5.4(5) ± .81	4.9(73) ± .15
Placental scars in uterus	4.7(8) ± .94	2.7(40) ± .36
Uterine loss (corpora lutea–embryos)	.25(4) ± .25	.29(47) ± .15

have greater uterine productivity than nonparasitized mice. This trend, of course, may not reflect actual success at birth or weaning. Sufficient data were not available to assess the effects of *Cuterebra* parasitism on reproduction in subadult female mice.

Mice parasitized by bot fly larvae had greatly enlarged spleens. The mean spleen weight for unparasitized subadult males was 345.9μg $\pm$ 7.9 (N = 285) and that for parasitized subadult males was 1277.2μg $\pm$ 167.7 (N = 18) ($p < .001$). The mean spleen weight for adult males without bots was 415.2μg $\pm$ 15.4 (N = 150) whereas that for parasitized adults was 1245.9μg $\pm$ 131.4 (N = 24) ($p < .001$). Spleen size in female mice was not considered as a valid assessment of the effect of *Cuterebra* on the spleen, because spleen size increases greatly during pregnancy (*see* Davis *et al.,* 1961).

DISCUSSION

Little information on egg-laying behavior in cuterebrids is available, but the few observations suggest that the females do not actively seek out the host to deposit eggs, but oviposit on sticks or blades of grass, especially at entrances to mammal burrows (Beamer *et al.,* 1943; Beamer, 1950; Catts, 1967; Dalmat, 1943). The larva hatches when a mouse encounters the egg. Hatching of eggs was induced in both *Cuterebra approximata* Walker and *C. latifrons* Coquillett by blowing human breath over the eggs (Catts, 1964). Eggs are probably deposited singly or in small groups rather than in large numbers at any one site (*see* Catts, 1964; Dalmat, 1943; Ferris, 1920), although *C. fontinella* may produce several hundred eggs. Catts (1967) has suggested that scattering the eggs decreases the possibility of their destruction by potential egg parasitoids or predators. Perhaps of even greater importance, by widely distributing the eggs the female increases the probability that a suitable host will encounter one or more eggs (Catts, 1967). Additionally, too many bots parasitizing a single mouse would decrease the probability of the host's survival; death for the host means death for these obligate parasites. In the less extreme case, it is to an individual larva's advantage to have a host for itself rather than compete with other larvae for resources from the host. Smith (1975) found that a single bot fly larva consumed 27 kcals, two bots consumed 47 kcals, and three bots consumed 61 kcals of energy during larval development. If two or three larvae are present, the average number of kilocalories each obtains is 23.5 and 20.3, respectively, which is only 87.0 and 75.3%, respectively, of the amount of energy a single bot obtains. Larvae from multiple infestations were smaller than those from single infestations (Smith, 1975). Larger size would probably confer an advantage in overwintering and in mating the following summer.

The mean infestation rate found during this study was 1.4 bots per infected mouse, with 69.1% of the parasitized mice having a single larva. *Cuterebra fontinella* was found on 9.2% of the white-footed mice trapped during July, August and September. Means of 1.2, 1.3 and 1.8 bots per infected mouse were reported from white-footed mice in Virginia (Hensley, 1976), Connecticut (Miller and Getz, 1969) and Michigan (Wecker, 1962). Smith (1975) found a mean of 1.1 larval *C. approximata* per parasitized mouse on deer mice (*Peromyscus maniculatus*) in Montana. Infestation rates ranging from 0.3% to 73% have been reported for *Peromyscus* (*see* Brown, 1965; Miller and Getz, 1969).

Natural hosts appear to have evolved a tolerance for *Cuterebra* parasitism. The genus *Cuterebra* is found only in the New World. When artificially infected with cuterebrid bot fly larvae under laboratory conditions, Old World murid rodents and rabbits experienced greater hardships and mortality than New World cricetid rodents and rabbits (Catts, 1965). Even when the hosts lived, larvae were seldom able to develop successfully in Old World hosts. Also, bots in those New World species that frequently harbor cuterebrids proved to be much more successful than those infesting New World hosts that do not naturally harbor *Cuterebra,* and bots in occasional hosts fared worse than those in primary hosts (Baird, 1971, 1972; Capelle, 1970; Catts, 1965; Gingrich and Barrett, 1976; Parker and Wells, 1919).

The presence of bot fly larvae on mice is a definite physiological stress (Payne and Cosgrove, 1966) and affects an individual's fitness. Smith (1975) subjected white-footed mice parasitized by *Cuterebra* to predation by short-tailed weasels (*Mustela erminea*). Mice carrying a single bot were no more susceptible to capture than healthy control mice; however, mice with two or more bots were at a disadvantage. In meadow voles [*Microtus pennsylvanicus* (Ord)], Getz (1970) found that voles with multiple infestations had a lower survival rate than voles with a single larva. With an abnormally high population of larval cuterebrids, the increase in predation on the host population could be important.

The parasite does not appear to jeopardize its primary host greatly. Larval *Cuterebra* significantly reduce the reproductive development of subadult male white-footed mice, but appear to have little effect on reproduction in either adult males or females. Reduced reproductive activity in a small percentage of males seemingly would be disadvantageous to those individuals, but the total reproductive output of the population probably would not be affected seriously.

For the cuterebrids, dispersing the eggs may help to ensure that an optimum number of offspring will encounter and develop on a host without killing the host. Concomitantly, white-footed mice have evolved an adaptive tolerance to bot fly larvae that minimizes the effects of parasitism.

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