

Impact of botfly parasitism on *Microtus townsendii* populations

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The impact of botfly (*Cuterebra grisea*) parasitism on populations of *Microtus townsendii* was studied on four areas near Vancouver, British Columbia, from 1971 to 1978. Botfly larvae were found in voles during the period from late June to late November, with a peak occurring from mid-August to mid-September. There was a significant negative relationship between vole density and the proportion of the population infested. The percentage of voles infested changed in the following manner in the three weight classes: juveniles (18.5%) > adults (16.5%) > subadults (13.0%), with the sexes showing no differences between them. Overall, noninfested voles always survived better than infested ones did in the three classes. In both adults and juveniles, survival declined as botfly larvae number increased; subadults did not show this relationship. Infested adult male voles survived more poorly at high densities ($r = 0.62$); adult females did not. Infested large adult males (≥ 55 g) survived better than small adults did (40–54 g), but the two size classes in females showed no survival differences. Infested adult voles had significantly lower rates of reproduction: 8% fewer males were in breeding condition, 10% fewer females were lactating, and 4% fewer females were pregnant. Parasitism significantly depressed growth rates in all weight classes above 40 g. We conclude that botflies had a significant detrimental influence on vole survival, reproduction, and growth.

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Les effets de l'œstre *Cuterebra grisea* ont été étudiés de 1971 à 1978 chez des populations de *Microtus townsendii* provenant de quatre régions voisines de Vancouver, Colombie Britannique. Les larves d'œstres se retrouvent chez les campagnols, de la fin de juin à la fin de novembre et leur nombre atteint un sommet de la mi-août à la mi-septembre. Il existe une corrélation négative significative entre la densité des campagnols et la proportion infestée de la population. Le pourcentage de campagnols infestés diffère chez les trois classes de poids: jeunes (18.5%) > adultes (16.5%) > sub-adultes (13.0%); les deux sexes sont affectés également. En général, les campagnols sains survivent mieux que les campagnols parasités, dans les trois classes. Chez les adultes et les jeunes, la survie diminue à mesure qu'augmente le nombre de larves parasites; cette relation n'existe pas chez les sub-adultes. Les campagnols adultes mâles, mais pas les femelles, ont une survie faible lorsque la densité de population est élevée ($r = 0.62$). Les mâles adultes de grande taille (≥ 55 g) survivent mieux que les adultes plus petits (40–54 g); cependant, chez les femelles, la survie est la même chez les deux classes de taille. Les campagnols adultes parasités ont des taux de reproduction significativement plus faibles: 8% moins de mâles sont en état de se reproduire, 10% moins de femelles allaitent et 4% moins de femelles deviennent enceintes. Le parasitisme diminue significativement les taux de croissance dans les classes de poids supérieures à 40 g. Il faut conclure que les œstres ont des effets nocifs significatifs sur la survie, la reproduction et la croissance des campagnols.

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Introduction

Many different rodent and lagomorph species in North America are annually parasitized by larvae of cuterebrid botflies (Smith 1977). In microtines, botfly infestations have been recorded only in *Microtus pennsylvanicus* (Buckner 1958; Clough 1965; Iverson and Turner 1968; Maurer and Skaley

1968; Getz 1970). During population studies on *M. townsendii* near Vancouver, British Columbia, extensive infestations of botflies (*Cuterebra grisea* Coq.)³ were found.

An infestation with botflies can potentially affect the fitness of the host through its effect on survival, reproduction, and growth. In this paper we will examine the significance of botfly parasitism on *M. townsendii* populations.

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Methods

Populations of *M. townsendii* were livetrapped on four different grassland areas near Vancouver: control grid C at the Serpentine Fen was trapped from 1971 to 1974; control grid E at the Ladner Airbase was trapped from 1971 to 1976; control grid I on Westham Island was trapped from 1971 to 1976; and control grids T.A and T.D and enclosures T.B and T.C on Reifel Island were trapped from 1976 to 1978. For a description of the first two sites see Krebs et al. (1976), for the third see LeDuc and Krebs (1975), and for the fourth see Beacham (1979a). *Cuterebra grisea* has previously been obtained from rodents caught in grassland habitat in southern Manitoba (Iverson and Turner 1968) and from rodents caught on recently logged sites in southwestern British Columbia (Hunter et al. 1972).

The general technique involved mark-and-recapture techniques by livetrapping with Longworth live traps for 2 days every 2nd week year around on areas that were either approximately 0.7 ha in size (grids C, E, and I) or approximately 0.3 ha in size (Reifel grids). A detailed description of the trapping technique can be found in LeDuc and Krebs (1975). In addition, pitfall traps (Boonstra and Krebs 1978) were employed on grid I in the summer of 1975 and on the Reifel grids from 1976 to 1978. The pitfall traps were trapped on a weekly basis and consecutively to the Longworth live traps. Animals caught in both trap types were treated in a similar manner. All voles were ear tagged and on each capture the following data were recorded: trap location, sex, sexual condition, weight, and number of botflies. Botflies were recorded from the summer of 1972 onwards. Animals were classified as adult (> 42 g), subadult (30–42 g), or juvenile (< 30 g).

Results

Period and frequency of occurrence

The percentage of voles infested and the population changes on grid I are shown in Fig. 1. The occurrence of these infestations is restricted to the summer and fall months, usually from the last week in July to the first week in November. On other areas, the period of occurrence was similar. The earliest occurrence was on 30 June 1977 on the grids on Reifel Island and the latest was on 27 November 1974 on grid I.

Figure 1 also shows that the maximum percentage of the population infested during a trapping session remained nearly constant each year, attaining a peak in middle to late August of between 25 and 35%. The largest percentage of the population infested during a trapping session occurred during the week of August 19, 1974 when 37.3% of the animals captured were infested. The other grids showed similar rates of infestation.

The infestation rate may change as a function of vole population density. Correlation analysis was carried out between the average population density in July and the maximum percentage of the population infested during a trapping session within that year, and between the average population density in July and the total percentage of the population infested over the entire season. The latter is the sum of the percentage of the population infested for

each trapping session over the entire season and gives a measure of the total infestation rate for that season. When all the grids are pooled, there is a significant negative correlation between average July density and the maximum percentage of the population infested ($r = -0.48$, $df = 19$, $P < 0.05$) and between average July density and the total percentage of the population infested ($r = -0.62$, $df = 17$, $P < 0.005$) (the degrees of freedom are smaller than in the previous analysis because trapping did not occur to the very end of the season in two cases). These results indicate that at higher densities, a smaller proportion of the population was infested with botflies.

The incidence of infestation may differ among the three weight classes. To examine this question, the numbers of animals caught in each of the three weight classes during the botfly season were summed. The botfly season is defined as that period between the detection of the first and last botfly infestation. Because sample size was too small in some classes (especially in the juvenile class), a number of years were pooled for a grid. Thus all the data for each of the classes for grid C, for grid E, and for grid I with the exception of 1975 were pooled. The use of pitfalls on grid I in 1975 and on the Reifel grids allowed sufficient sample sizes to be obtained in each year. Heterogeneity chi-square analysis was then performed. Although the total chi-square and the pooled chi-square were significant for both sexes, so was the heterogeneity chi-square (Table 1). This occurred because the magnitude of the difference between the age classes for each of the grids was not the same nor was the direction of the difference always the same. In general, however, a slightly higher proportion of juveniles was parasitized than was the proportion of adults, which in turn was higher than for subadults. There was no significant difference in the incidence of parasitism within a class between sexes for all the data pooled (adult males vs. adult females, $\chi^2 = 0.003$; subadult males vs. subadult females, $\chi^2 = 0.43$; juvenile males vs. juvenile females, $\chi^2 = 0.96$).

Survival

We examined whether there was any effect on survival by summing the number of animals surviving and those not surviving each 2-week trapping interval over the whole botfly season for infested and noninfested animals and calculated a mean survival rate. Heterogeneity chi-square analysis was then performed. In adults, adequate samples could be obtained in each year for infested and noninfested animals. In subadults and ju-

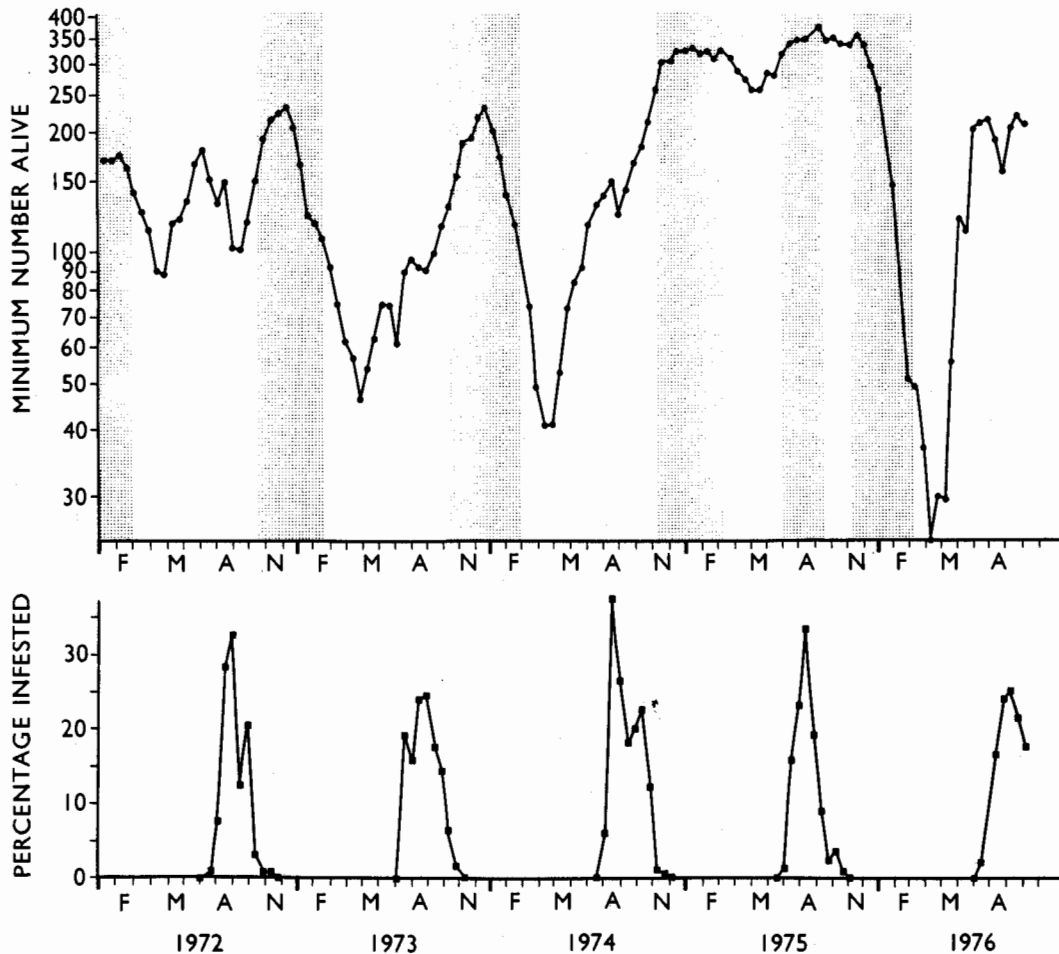


FIG. 1. Population changes in *M. townsendii* on grid I, Westham Island, from 1972 to 1976 and changes in the frequency of parasitism by botflies.

veniles, the sample sizes for any one year were often very small so that several years of data for a grid were pooled as indicated in the tables.

Adults

Adult males (Table 2) without botflies had an overall advantage of 0.10 survival rate per 2 weeks over animals with botflies (a 16% advantage). In 16 of 21 grid-year comparisons (a grid-year was 1 grid trapped for 1 year) animals without botflies survived better than animals with botflies.

Results were similar in adult females. Females generally survived better than males (an overall advantage of about 0.05 survival rate per 2 weeks) and females without botflies had an advantage of 0.10 survival rate per 2 weeks over females with botflies (a 15% advantage). In 17 of 21 grid-year comparisons the noninfested females survived better.

Subadults

Subadult noninfested males had an advantage of 0.09 survival rate per 2 weeks (a 16% advantage) (Table 3). There was a large amount of variability in the subadult data. In 5 of 12 grid-year comparisons infested voles survived slightly better than noninfested ones, though in no single comparison was this significant.

Results were similar in subadult females, with noninfested animals having an advantage of 0.07 survival rate per 2 weeks (an 11% advantage). All chi-square values were significant, indicating pronounced differences between grids. In 4 of 12 grid-year comparisons infested voles survived slightly better, but again none of these was significant statistically.

Juveniles

Noninfested juveniles also had an overall ad-

TABLE 1. Proportion of voles parasitized among three size classes of *Microtus townsendii*. The data for all years were pooled for grids C, E, and I as described in the text. Sample size in parentheses

Grid	Year	Males				Females			
		Adults	Subadults	Juveniles	χ^2	Adults	Subadults	Juveniles	χ^2
C		0.27 (626)	0.17 (218)	0.21 (100)	8.40	0.19 (703)	0.17 (410)	0.25 (123)	4.06
E		0.19 (720)	0.12 (513)	0.15 (113)	10.41	0.17 (700)	0.11 (510)	0.135 (207)	9.06
I		0.15 (1387)	0.11 (180)	0.10 (68)	3.28	0.11 (1995)	0.06 (448)	0.06 (108)	4.23
I	(1975)	0.12 (1511)	0.07 (404)	0.07 (72)	9.22	0.16 (1364)	0.09 (755)	0.06 (81)	23.08
T.A	(1976)	0.24 (140)	0.33 (39)	0.20 (59)	2.17	0.21 (214)	0.28 (46)	0.13 (52)	3.26
T.A	(1977)	0.12 (495)	0.15 (205)	0.19 (89)	3.99	0.16 (602)	0.12 (280)	0.14 (137)	10.38
T.B	(1976)	0.29 (237)	0.23 (127)	0.30 (174)	2.14	0.24 (371)	0.22 (149)	0.29 (175)	2.35
T.B	(1977)	0.08 (635)	0.08 (352)	0.09 (161)	0.42	0.18 (441)	0.11 (386)	0.13 (132)	7.53
T.C	(1976)	0.32 (117)	0.32 (94)	0.33 (135)	0.05	0.24 (238)	0.31 (129)	0.31 (162)	2.80
T.C	(1977)	0.17 (485)	0.11 (319)	0.14 (126)	6.36	0.19 (422)	0.12 (445)	0.10 (177)	11.15
T.D	(1976)	0.29 (209)	0.42 (65)	0.41 (71)	5.29	0.26 (315)	0.22 (60)	0.34 (50)	2.20
T.D	(1977)	0.14 (514)	0.08 (243)	0.07 (103)	7.14	0.17 (549)	0.10 (270)	0.05 (93)	15.12
Totals		0.16 (7076)	0.13 (2759)	0.19 (1272)	27.65	0.17 (7914)	0.13 (3798)	0.18 (1505)	36.66
Total χ^2				(df = 12)	58.87**				95.22**
Pooled χ^2				(df = 1)	27.65**				36.66**
Heterogeneity χ^2				(df = 11)	31.22*				58.56**

NOTE: *, $p < 0.01$; **, $p < 0.001$.TABLE 2. Minimum survival rates per 14 days for adult *Microtus townsendii* with and without botfly infestations. Sample size in parentheses

Grid	Year	Males			Females		
		N_m Infested	Noninfested	χ^2	N_m Infested	Noninfested	χ^2
C	1972	0.878 (90)	0.917 (36)	0.39	0.857 (77)	0.750 (20)	1.32
	1973	0.833 (240)	0.881 (59)	0.82	0.890 (318)	0.934 (61)	1.10
	1974	0.820 (128)	0.808 (73)	0.04	0.925 (173)	0.852 (54)	2.61
E	1972	0.843 (51)	0.800 (15)	0.16	0.940 (32)	0.920 (13)	0.03
	1973	0.803 (76)	0.800 (20)	0.00	0.848 (66)	0.895 (19)	0.26
	1974	0.827 (98)	0.786 (28)	0.24	0.928 (138)	0.900 (30)	0.26
	1975	0.895 (294)	0.889 (54)	0.02	0.894 (218)	0.857 (35)	0.43
	1976	0.834 (65)	0.763 (19)	0.49	0.878 (125)	0.885 (24)	0.01
I	1972	0.767 (275)	0.652 (46)	2.79	0.831 (415)	0.578 (45)	16.72
	1973	0.803 (234)	0.689 (45)	2.93	0.860 (342)	0.723 (47)	5.80
	1974	0.800 (501)	0.632 (68)	9.86	0.855 (740)	0.793 (87)	2.36
	1975	0.645 (1324)	0.337 (187)	65.17	0.651 (1145)	0.430 (219)	37.95
	1976	0.934 (166)	0.711 (52)	18.61	0.766 (282)	0.621 (37)	3.63
T.A	1976	0.471 (106)	0.365 (34)	1.17	0.722 (169)	0.678 (45)	0.35
	1977	0.737 (437)	0.676 (58)	0.97	0.773 (505)	0.723 (97)	1.13
T.B	1976	0.620 (168)	0.659 (69)	0.33	0.805 (282)	0.835 (89)	0.49
	1977	0.751 (582)	0.509 (53)	14.49	0.727 (364)	0.719 (77)	0.08
T.C	1976	0.389 (79)	0.566 (38)	3.26	0.747 (180)	0.634 (58)	2.73
	1977	0.709 (401)	0.749 (84)	0.47	0.733 (343)	0.666 (79)	1.62
T.D	1976	0.615 (148)	0.561 (61)	0.19	0.777 (233)	0.562 (82)	14.04
	1977	0.744 (444)	0.583 (70)	7.79	0.752 (456)	0.628 (93)	6.09
Totals		0.735 (5907)	0.636 (1169)	46.90	0.784 (6603)	0.683 (1311)	62.04
Total χ^2			(df = 21)	130.19***			99.01***
Pooled χ^2			(df = 1)	46.90***			62.04***
Heterogeneity χ^2			(df = 20)	83.29**			36.97*

NOTE: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

TABLE 3. Minimum survival rates per 14 days for subadult *Microtus townsendii* with and without botfly infestations. All years for grid C, for grid E, and years 1972 to 1974 and 1976 for grid I pooled. Sample size in parentheses

Grid	Year	Males			Females		
		Noninfested	Infested	χ^2	Noninfested	Infested	χ^2
C	(Pooled)	0.789 (180)	0.684 (38)	1.94	0.862 (340)	0.914 (70)	1.42
E	(Pooled)	0.835 (451)	0.855 (62)	0.16	0.880 (453)	0.808 (57)	2.37
I	(Pooled)	0.731 (160)	0.429 (20)	6.70	0.775 (320)	0.679 (28)	1.34
I	1975	0.580 (374)	0.321 (30)	6.78	0.628 (685)	0.297 (70)	28.91
T.A	1976	0.270 (26)	0.398 (13)	0.65	0.591 (33)	0.441 (13)	0.85
T.A	1977	0.677 (175)	0.608 (30)	0.55	0.634 (247)	0.606 (33)	0.10
T.B	1976	0.560 (98)	0.446 (29)	1.17	0.608 (117)	0.631 (32)	0.06
T.B	1977	0.648 (322)	0.540 (30)	1.38	0.560 (344)	0.523 (42)	0.21
T.C	1976	0.490 (64)	0.557 (30)	0.36	0.649 (89)	0.557 (40)	1.01
T.C	1977	0.680 (284)	0.549 (35)	2.42	0.625 (390)	0.644 (55)	0.08
T.D	1976	0.353 (38)	0.446 (27)	0.58	0.464 (47)	0.308 (13)	1.04
T.D	1977	0.664 (223)	0.800 (20)	1.54	0.628 (254)	0.696 (26)	0.47
Totals		0.678 (2395)	0.585 (364)	12.19	0.691 (3319)	0.621 (479)	9.36
Total χ^2			(df = 12)	24.23*			37.86***
Pooled χ^2			(df = 1)	12.19***			9.36**
Heterogeneity χ^2			(df = 11)	12.04			28.50**

NOTE: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.TABLE 4. Minimum survival rates per 14 days for juvenile *Microtus townsendii* with and without botfly infestations. All years for grid C, for grid E, and for grid I pooled. Sample size in parentheses

Grid	Year	Males			Females		
		Noninfested	Infested	χ^2	Noninfested	Infested	χ^2
C	(Pooled)	0.734 (79)	0.667 (21)	0.38	0.696 (92)	0.613 (31)	0.72
E	(Pooled)	0.808 (96)	0.824 (17)	0.02	0.797 (179)	0.664 (28)	2.49
I	(Pooled)	0.512 (129)	0.386 (12)	0.25	0.584 (177)	0.650 (12)	0.20
T.A	1976	0.239 (47)	0.344 (12)	0.51	0.619 (45)	0.741 (7)	0.41
T.A	1977	0.718 (72)	0.247 (17)	13.06	0.707 (104)	0.508 (33)	2.35
T.B	1976	0.594 (122)	0.570 (52)	0.08	0.517 (125)	0.822 (50)	6.03
T.B	1977	0.420 (145)	0.569 (16)	1.30	0.496 (115)	0.374 (17)	0.84
T.C	1976	0.404 (90)	0.571 (45)	3.43	0.542 (112)	0.517 (50)	0.26
T.C	1977	0.667 (109)	0.435 (17)	3.41	0.611 (160)	0.300 (17)	6.09
T.D	1976	0.262 (42)	0.275 (29)	0.02	0.342 (33)	0.484 (17)	0.92
T.D	1977	0.532 (96)	0.600 (7)	0.11	0.581 (88)	0.200 (5)	2.78
Totals		0.551 (1027)	0.513 (245)	1.39	0.611 (1230)	0.562 (267)	2.56
Total χ^2			(df = 11)	22.57*			23.09*
Pooled χ^2			(df = 1)	1.39			2.56
Heterogeneity χ^2			(df = 10)	21.18*			20.53*

NOTE: *, $p < 0.05$.

vantage over infested animals (in males an advantage of 0.04 survival rate per two weeks, a 7% advantage; in females an advantage of 0.05 survival rate per 2 weeks, a 9% advantage) (Table 4). In 6 of 11 grid-year comparisons in males, infested voles survived better than noninfested voles and in females this was 4 out of 11. Botflies, therefore, appear to have less of an effect on juvenile survival, probably because juvenile survival was already typically poor in comparison with adult survival.

Survival versus number of botfly larvae

We examined whether the number of larvae per vole affects survival. All the data from all the grids were pooled and the minimum 2 week survival rates calculated for animals with one, two, and three or more botfly larvae. There is a significant depression in survival in both adults and juveniles of both sexes with an increased number of larval parasites (Table 5). Adult males with one larva had a survival advantage of 0.16 survival rate per 2 weeks (a 31%

TABLE 5. Minimum survival rates per 14 days for voles with different numbers of botfly parasites. Data were pooled for all grids and years. Sample size in parentheses

	Males				Females			
	No. parasites			χ^2	No. parasites			χ^2
	1	2	≥ 3		1	2	≥ 3	
Adults	0.669 (731)	0.585 (290)	0.511 (148)	16.27**	0.705 (826)	0.712 (305)	0.533 (180)	21.82**
Subadults	0.611 (264)	0.519 (74)	0.550 (26)	2.21	0.626 (349)	0.606 (90)	0.610 (40)	0.15
Juveniles	0.584 (143)	0.439 (61)	0.370 (41)	7.52*	0.646 (165)	0.554 (59)	0.284 (43)	18.30**

NOTE: *, $p < 0.05$; **, $p < 0.001$.

advantage) over males infested with three or more larvae; in females there was an advantage of 0.17 survival rate per 2 weeks (a 32% advantage). In juveniles, this relationship was even more marked: males with one larva had a survival advantage of 0.21 survival rate per 2 weeks (an advantage of 58%) over juveniles infested with three or more larvae; in females there was an advantage of 0.36 survival rate per 2 weeks (an advantage of 128%). Neither subadult males nor females showed a significantly depressed survival with increased larval number.

Survival versus population density

The effect of botfly infestation may change as a function of density and the reproductive state of the population. To examine what factors might influence the impact of a botfly infestation, we carried out multiple regression analysis using as the dependent variable an overall survival advantage, which was calculated for each year for each grid as (noninfested survival rate - infested survival rate) for adult males and females only during the period in which $\geq 10\%$ of the population was infested, and the following as independent variables: the average population density in July (the usual start of the botfly season); the percentage of breeding adult males during the same period in which the survival advantage was measured; the percentage of lactating adult females in the same period; and the maximum percentage of the population infested during a trapping session within the year. In adult males survival advantage was related to average July density ($r = 0.62$, $n = 21$, $P < 0.005$); none of the other variables significantly explained any more of the variance. There was no relationship in adult females between survival advantage and any of the variables.

Survival versus adult body size

Boonstra and Krebs (1979), in an analysis to examine the survival advantage of large body size in adults of four species of *Microtus*, found that *M. townsendii* was the only species in which the adaptive value of large size differed between the sexes. Large adult female *M. townsendii* were always at a survival disadvantage with respect to small adult females. To examine whether poorer survival in large adult females could be caused by botfly parasitism, adults were divided by weight as follows: small adults were defined as those between 40 and 54 g and large adults were greater than 54 g. The survival rates of only the parasitized animals in these age classes were then calculated. Large adult males were parasitized significantly more than small ones, but these animals still had better survival rates (Table 6). Large adult females were also more heavily parasitized than small adult females although the difference between the two was only 0.02 and the heterogeneity chi-square was significant indicating considerable variance between grids. There was no overall difference in the survival rate between the two size classes (pooled chi-square not significant). Therefore adult females gain no advantage from large size when parasitized, whereas adult males do. We conclude that parasitism does not put large females at a survival disadvantage with respect to small adults so the relationship found by Boonstra and Krebs (1979) cannot be explained by botflies.

Reproduction

We determined whether the presence of botflies depressed reproduction by examining the data for adult animals during the trapping sessions when the percentage of the vole population infested with botflies was $\geq 10\%$. For each grid and year, the

TABLE 6. Frequency of parasitism and minimum survival rates per 14 days for large (≥ 55 g) and small (40–54 g) adult *M. townsendii* for all the data pooled. Sample size in parentheses

	Males		Females	
	Large	Small	Large	Small
Frequency of parasitism	0.19 (3522)	0.14 (4318)	0.18 (4064)	0.16 (4868)
Total χ^2 (df = 11)		42.35***		28.34**
Pooled χ^2 (df = 1)		39.96***		7.00**
Heterogeneity χ^2 (df = 10)		2.39		21.34*
Survival rate				
of parasitized animals	0.671 (676)	0.578 (600)	0.684 (715)	0.661 (755)
Total χ^2 (df = 11)		37.61***		38.91***
Pooled χ^2 (df = 1)		11.68***		0.89
Heterogeneity χ^2 (df = 10)		25.93**		38.02**

NOTE: *, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

total number of animals in various states of reproductive condition (for males the position of the testes; for females lactating or not and obviously pregnant or not) was summed for infested and noninfested animals.

In adult males, 8% more noninfested animals were in breeding condition than infested animals (Table 7). The heterogeneity chi-square was significant because although a larger percentage of noninfested males were in breeding condition than infested males in 19 out of 21 comparisons, there were changes in the magnitudes of the differences among the years and grids. In adult females, 10% more noninfested animals were found to be lactating than infested animals (17 out of 21 comparisons) (Table 7). With respect to obvious pregnancies, 4% more noninfested females were pregnant than infested females (in 15 of the comparisons, more noninfested animals were pregnant; in 2 of the comparisons there was no difference). We conclude that the presence of botfly larvae significantly depressed the reproductive fitness of both adult males and females.

Growth

We examined whether botflies affect growth by analyzing the instantaneous growth rates of voles during the botfly seasons on all the grids. However, since not all grids were trapped each year, the analysis of covariance was unbalanced. We divided the voles into four weight classes (< 40 g, 40–49 g, 50–59 g, and > 59 g) and calculated their instantaneous growth rates in percent per day between trapping weeks (growth rates derived from captures more than 4 weeks apart were excluded). Obviously pregnant females were excluded from the analysis. We analyzed the data by a five-way analysis of covariance with growth rate as the

dependent variable, weight as the covariate, the sex, grid, year, group (infested or noninfested), and weight class as the five indices.

All of the main effects in this analysis were significant. In particular we are interested in the comparison between infested and noninfested animals ($F = 13.9$, $df = 1$, 9777 , $P < 0.001$). There was also a significant interaction between infestation and weight class ($F = 610$, $df = 3$, 9777 , $P < 0.001$). The interaction between group and weight class occurred because infested voles under 40 g grew better than noninfested voles did, whereas in all other weight classes, infested voles always had lower growth rates (Fig. 2). Therefore, in general, infested voles grew more slowly than noninfested voles did.

Discussion

Botfly parasitism has a significant immediate impact on the demography of *M. townsendii* populations: survival is depressed, reproduction is reduced, and growth rate is retarded. An indication of the biological significance of these results can be obtained from simple calculations of the mean expectation for further life. For example, the mean expectation for further life for noninfested adult males was 6.50 weeks compared with 4.46 weeks for infested males. Other classes of animals showed similar differences between infested and noninfested animals. These large differences in survival plus the reduction in reproduction and growth (in all animals above 40 g) result in infested voles being significantly less fit than noninfested voles.

The consistently lower survival rates of infested *M. townsendii* found in our study (Tables 2, 3, 4) differ from those found on *M. pennsylvanicus*. Iverson and Turner (1968) found that infested voles of this species survived no differently from nonin-

TABLE 7.^a Intensity of reproduction in infested and noninfested adult *Microtus townsendii* during trapping sessions in which $\geq 10\%$ of the population was infested summed over all trapping grids and years. Sample sizes in parentheses

	Percentage of females					
	Percentage of males breeding		Lactating		Pregnant	
	Noninfested	Infested	Noninfested	Infested	Noninfested	Infested
Totals	51 (2281)	43 (832)	26 (2828)	16 (931)	7 (2828)	3 (931)
Total χ^2 (df = 21)	98.50*					28.70
Pooled χ^2 (df = 1)	17.96*					18.59*
Heterogeneity χ^2 (df = 20)	80.54*					10.11

NOTE: * $p < 0.001$.

^aThe complete table containing the data for each grid and year is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2.

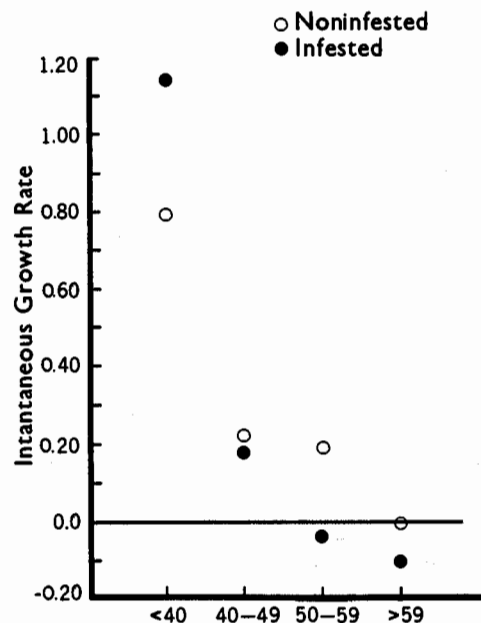


FIG. 2. Instantaneous growth rates in percent per day of *M. townsendii* infested with botflies and of those not infested for all the data pooled.

infested voles, whereas Getz (1970) found that infested voles survived slightly better (though not significantly so). The cause for these differences between *M. townsendii* and *M. pennsylvanicus* is unknown but may in part be related to the relatively small sample sizes of infested voles in the studies on the latter species (65 infested voles in the study of Iverson and Turner and 47 in the study of Getz).

Field studies on *Peromyscus* species have found no consistent effect of botfly infestations on survival, but again in some of these studies, sample sizes were small. *Peromyscus* infested with botflies have been found to survive better than (Wecker 1962; Goertz 1966), similar to (Hunter et al. 1972), or worse than (Miller and Getz 1969) noninfested animals.

Both Clough (1965) and Iverson and Turner (1968) found almost no female *M. pennsylvanicus* pregnant when they were parasitized by botflies. Getz (1970), however, found pregnancy rates of up to 49% in parasitized females. The cause for these differences is unknown. Even if these females can successfully give birth, they may have difficulty rearing the young. Sillman (1955) found that none of the four litters born by parasitized *Peromyscus leucopus* was successfully reared. However, Timm and Cook (1979) found no reduction in the number of embryos, corpora lutea, or placental scars in adult females of this species parasitized by botflies

compared with nonparasitized females, indicating that parasitized females suffered no depression in reproduction. These results differ markedly from those found in our study in *M. townsendii* in which adult female reproduction is severely depressed.

Emasculatation in males may be caused by one or more botfly larvae in the inguinal region (Dunaway et al. 1967). Getz (1970) found that *M. pennsylvanicus* were only emasculated when two or more botfly larvae were found in the inguinal region. Timm and Cook (1979) found similar results in adult *P. leucopus*; males with one botfly larva showed no reduction in testes size, whereas those with two or more had smaller testes. Parasitized subadult males always had smaller testes, epididymides, and seminal vesicles, though this did not affect the presence of sperm. In our study, 8% fewer parasitized males were in breeding condition (as assessed by descended testes) than were nonparasitized males. The reduction in size of the testes may significantly alter the social relationships among breeding males, since the reduction of circulating androgens during the complete or partial emasculation period would affect behavior (Davidson and Levine 1972). This in turn might have repercussions on survival.

Lower growth rates in parasitized voles might also have secondary effects on survival. Heavier animals are generally dominant over lighter ones in encounters (Turner and Iverson 1973). In our study, parasitized animals in all weight classes above 40 g grew more slowly. Infested animals under 40 g grew faster. This may partly be explained by the growth of the botfly larvae, which can reach a weight of 0.69 g (Iverson and Turner 1968). In *M. pennsylvanicus*, Clough (1965) found that in a sample of 18 males, parasitized mice were heavier, whereas his sample of 12 parasitized females was lighter. However, he did not take into account the age of his mice. Iverson and Turner (1968), who accounted for age, found that parasitized voles weigh less than nonparasitized voles. Thus depression of growth may be a general result of botfly parasitism in microtines.

Botfly infestations can cause severe pathological conditions in rodents. Anemia, leucocytosis, and plasma protein imbalances have been found in *Peromyscus leucopus* infested with botflies (Sealand 1961; Dunaway et al. 1967; Timm and Cook 1979). Clough (1965) found lighter thymus glands and heavier spleens in *M. pennsylvanicus* infested with botflies. However, in the latter study, the stress of cold water immersion was not aggravated by botfly infestations. We found that the stresses of high density in *M. townsendii* added to the stress of

botfly infestation only in adult males and that this was not further aggravated by reproductive state of the population. The survival rate of infested adult females was not affected by either density or the reproductive condition of the population. Why the two sexes differ in this respect remains a puzzle.

The exact cause of the poorer survival seen in parasitized voles is unknown. Parasitized mice may move about with greater difficulty and be more susceptible to predation (Dunaway et al. 1967; Smith 1978a). However, Smith (1978b) found *P. maniculatus* infested with one botfly were no more susceptible to weasel predation than the noninfested mice. Some of the greatest survival differentials between noninfested and infested voles occurred on Westham and Reifel Islands (Tables 2, 3, 4) where no weasels have ever been captured (Boonstra 1977a; Beacham 1979b), whereas at Ladner Airbase and the Serpentine Fen, where weasels are present, the survival differentials were generally only slight or not present. Weasels were therefore not the cause of the poorer survival rates of parasitized voles. Other predators were either rare or absent during the height of the botfly season on all areas.

Some of the poorer survival in infested voles could be due to a secondary infection with the grey flesh fly (*Wohlfahrtia vigil*) (Boonstra 1977b). Any animal parasitized by this fly is almost certain to die. However, the incidence of parasitism during any trapping session was so low that it cannot account for the poor survival rates seen in botfly-infested voles.

Poor survival is probably related to the size and reproductive status of the vole infested. Juveniles were severely affected by multiple infestations (Table 5). Adults were generally the only animals that reproduced, and multiply infested animals here too were severely affected. Subadults, which are intermediate in size and do not reproduce, were not affected by multiple infestations. However, these two variables are not the sole explanations for the poor survival in infested animals, because even subadults with botflies survive significantly worse than animals with no botflies (Table 3). The cause of the mortality must therefore be directly related to the pathology associated with the infestation.

The botfly *Cuterebra grisea* appears to be a well adapted parasite in some species of rodents such as in *Peromyscus maniculatus* (Hunter et al. 1972), having little or no effect on survival. However, in our study a pronounced negative effect was found. Hunter and Webster (1973) suggest that *Microtus* may be less "natural" hosts than *Peromyscus*. In

Peromyscus, the final larval stages are generally found in the inguinal regions (approximately 96% of the time), whereas in a study involving *M. pennsylvanicus*, only 37% were inguinally situated and the remainder were on the sides, chest, back, head, and abdomen (Getz 1970). Lack of site specificity of the mature botfly larvae may be an indication of a poorly adapted parasite to its host. No record was kept of where the larvae were situated in our study, but they were often seen on the sides, back, and at the base of the neck, though the majority were situated inguinally. If this species of cuterebrid is poorly adapted to *M. townsendii*, this may explain the poorer survival rates of infested voles.

The majority of microtine species studied to date have shown a more or less typical 2–4 year cycle in population numbers accompanied by a set of relatively consistent demographic characteristics (Krebs and Myers 1974). The majority of the *M. townsendii* populations do not show these cycles although they do show many of the demographic characteristics (LeDuc and Krebs 1975; Krebs et al. 1976; Krebs 1979) (for a study in which the species did cycle, see Beacham 1979a). It is possible that if genetic selection is occurring in this species, these annual bouts of parasitism disrupt the selection process and alter the population demography. However, the data on the LAP locus (LeDuc and Krebs 1975; Krebs et al. 1976) do not show any consistent change in gene frequencies during the period of parasitism. We are unable to test the intriguing hypothesis that botfly parasitism differentially eliminates the socially dominant voles in *M. townsendii*. Therefore it is likely that the acyclic nature of this species is due to other factors.

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