



BOT FLY PARASITISM (ROGENHOFERA BONAERENSIS) (DIPTERA, CUTEREBRIDAE) IN THE PAMPEAN GRASSLAND MOUSE (AKODON AZARAE), IN ARGENTINA

Authors: Zuleta, Gustavo A., and Vignau, María Laura

Source: Journal of Wildlife Diseases, 26(1) : 11-17

Published By: Wildlife Disease Association

URL: <https://doi.org/10.7589/0090-3558-26.1.11>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

BOT FLY PARASITISM (*ROGENHOFERA BONAERENSIS*) (DIPTERA, CUTEREBRIDAE) IN THE PAMPEAN GRASSLAND MOUSE (*AKODON AZARAE*), IN ARGENTINA

Gustavo A. Zuleta^{1,3} and Maria Laura Vignau²

¹ Departamento de Microbiología, Facultad de Medicina, Universidad Nacional de Buenos Aires, Paraguay 2155, Piso 14, Buenos Aires, 1121, Argentina

² Cátedra de Parasitología, Facultad de Ciencias Veterinarias, Universidad Nacional de La Plata, Calle 60 y 118, La Plata, 1900, Argentina

³ Present address: Area Ecología, Departamento de Biología, Ciudad Universitaria, Pab. II, 4° p., Buenos Aires, 1428 Argentina

ABSTRACT: Seasonality and impact of parasitism by the larvae of *Rogenhofera bonaerensis* (Diptera: Cuterebridae) in pampean grassland mouse (*Akodon azarae*, Rodentia, Cricetidae) populations were studied in grasslands and cropfield borders near Diego Gaynor (Buenos Aires Province, Argentina), from November 1985 to December 1986. Trapped mice infections ranged from one larva (77%) to four (4%) per host; larvae occurred on tails (75.7%), backs (17.1%), thighs (5.7%), and abdomen (1.4%). Prevalence of larvae occurred in late spring (November and December) (35%), and in fall (March to June) (20%), with a peak of 25% during April and May. In spring these larvae affected 46% of resident and 19% of transient individuals; however, no differences were found between residents and transients in spring or fall. There was no significant relationship between mouse population density and prevalence of parasitism ($r = -0.56$). The annual percentage of infected rodents changed with age (body size classes): adults (37%) > subadults (25%) > juveniles (16%); with no differences between the sexes. Similar results were recorded in the spring, but there were no differences in the fall. Significant differences were not detected between stable (22% infected) and disturbed habitats (14% infected). During winter uninfected mice survived better than those infected during the previous fall. In contrast, the summer survival among spring infected mice and noninfected mice was similar. Parasitism showed no effects on reproductive activity and on home range size. Larvae showed strong host specificity for *A. azarae* (99%). Only one case was recorded in the long-tailed mouse (*Oligoryzomys flavescens*), and none in the white paunch mouse (*Calomys laucha*), both species sympatric with *A. azarae*. This suggests that the pampean grassland mouse is essential for perpetuation of this bot fly as a result of a coevolutionary process within the grassland rodent assemblage. According to the *A. azarae* population dynamics the bot fly strategy could be adjusted to an opportunist pattern.

Key words: Host-parasite relationship, bot fly, prevalence, survival, impact of parasitism, Cuterebridae, *Akodon azarae*, *Rogenhofera bonaerensis*, reproduction, home range, ecology.

INTRODUCTION

Bot fly larvae of the family Cuterebridae cause cutaneous myiasis in rodents, lagomorphs and primates in the New World; it occurs secondarily in domestic animals and humans. Many studies have examined the impact of these flies on rodent populations in the Nearctic region (Sealand, 1961; Wecker, 1962; Payne et al., 1965; Dunaway et al., 1967; Bennett, 1972; Hunter et al., 1972; Baird, 1974; Smith, 1978; Boonstra et al., 1980; Catts, 1982), but little is known from the Neotropical region. Studies on the Neotropical cuterebrid *Rogenhofera bonaerensis* have been only on its morphology (Del Ponte,

1939). Life history and host-parasite relationship data are not available.

Rogenhofera spp. have been reported only in Peru, Brazil and Argentina. In Argentina this genus has been reported from *Oligoryzomys flavescens*, *Sciurus aestuans* and *Reithrodon physodes* (Berg, 1876; Lynch Arribalzaga, 1881; Del Ponte, 1959). The presence of *R. bonaerensis* in *Akodon azarae* is advantageous for the bot fly because *A. azarae* is a common and ecologically diverse rodent species in Argentina (Crespo, 1966; Pearson, 1967; Dalby, 1975; Kravetz, 1978; De Villafañe, 1981; Busch, 1987; Zuleta, 1989).

The purpose of this paper was to (1)

analyze the seasonality of parasitism, (2) examine the impact on rodent fitness, and (3) determine the host specificity of the cuterebrid fly larvae, *R. bonaerensis*, in the pampean grassland mouse (*A. azarae*) in Argentina.

MATERIALS AND METHODS

Akodon azarae populations were live-trapped on a 1 ha grassland and a 200-m corn field border near Diego Gaynor (34°17'S, 59°15'W; Buenos Aires Province, Argentina), November 1985 to December 1986. This grassland showed a seasonal succession in dominance by gramineous (*Stipa* spp., *Paspalum* sp., *Briza* sp.) and composite species (*Senecio grisebachii* and *Baccharis* sp.).

The sampling technique involved mark-and-recapture with Sherman live traps for 6 days every month. Trap arrangement varied according to the habitat: in the grassland a 7.5 m grid was established, and in the corn field border an assessment line with similar distances between stations was used. Each station was represented by a single trap. Traps were baited with peanut butter and examined twice a day (9 A.M.; 9 P.M.). The overall trapping effort was 20,821 trap examinations.

All animals were toe-clipped, and at each capture the following data were recorded: trap location, species, sex, reproductive condition (active or non-active), total length, tail length and evidence of cuterebrid parasitism. Animals were classified as residents or transients based upon the spacing behavior (Brown and Orians, 1970) by capture probability (Zuleta, 1984). According to the linear regression between body size and age (Zuleta, 1989), the following age classes were estimated: juveniles (<4 mo), subadults (4 to 5 mo), adults (>5 mo).

Survivorship curves were constructed ($l_x = N_t/N_0$, where l_x was the proportion of animals living to age x ; N_0 was the initial number of animals; and N_t was the number living to age x), and the likelihood ratio (LR) test (Gross and Clark, 1975) was applied to compare them (Pyke and Thompson, 1986). Life expectancy (e) was calculated as the mean age at death of the members of a group (Caughley, 1977). Independence G-analysis (Sokal and Rohlf, 1979) was performed to test the relationship between prevalence of bot fly larvae and associated variables such as sex, age, spacing behavior and reproduction activity. Minimum number alive (Krebs, 1966) was used to estimate density. The boundary strip inclusive method (Blair, 1940; Stickel, 1954) was performed to estimate home range for each mouse with four or more captures. Kruskal-Wallis one-way tests (Hollander &

Wolfe, 1973) were applied to compare home range areas.

Taxonomic identification of the bot flies was based upon the description of adults by Del Ponte (1939). These were obtained from larvae which were reared to pupae and emerged as adults under laboratory conditions.

RESULTS

Wound localization

From a sample size of 47 mice the third instar development sites of *R. bonaerensis* occurred in the dorsal to the base of the tail (76%), on the back, near the tail (17%), in the thigh (6%), and in the abdomen (1%). Percentages of hosts infected with one, two, three and four bot fly larvae were 77, 15, 4 and 4%, respectively.

Seasonality and density

Prevalence of *R. bonaerensis* showed two seasonal phases (Fig. 1) in the annual mouse cycle (Fig. 2): (1) in late spring (November to December) there was 26% in 1985 ($n = 81$) and 48% ($n = 48$) in 1986, and (2) in fall (March to June) there was 20% in 1986 ($n = 448$), with a maximum in April to May (25%, $n = 279$). During March and June the prevalence was near 10%. Infected animals were not recorded during January, February, July, August and September. Statistical differences obtained between seasons were (1) fall versus spring 1986 ($G = 19.28$; $P < 0.001$; $n = 506$), and (2) 1985 spring versus 1986 spring ($G = 6.43$; $P < 0.02$; $n = 139$). The prevalence of bot fly larvae showed no dependence on density according to the linear regression model ($r = -0.56$, $b = 0.19$ (ANOVA F -test) $F = 2.71$, $P < 0.15$).

Impact of parasitism

Significant differences in prevalence were noted across the age classes of juveniles < subadults < adults for the entire study period and the spring period alone (Table 1). There was not a significant difference in prevalence across age classes in fall.

There was no relationship between spacing behavior and parasitism ($G = 0.89$, n

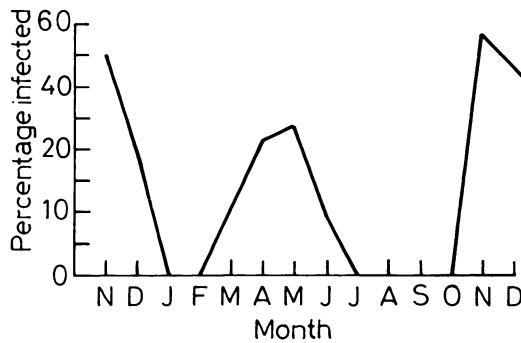


FIGURE 1. Monthly prevalence of *Rogenhofera bonaerensis* in *Akodon azarae* from Argentina (1985–1986).

= 199). The prevalence for resident and transient animals was 30% ($n = 83$) and 24% ($n = 116$), respectively. The percentage of infected mice changed during the spring, 46% for residents ($n = 24$) and 19% for transients ($n = 31$), but the difference is not statistically significant. There was an increase in prevalence of bot fly larvae with habitat stability from 14% ($n = 94$) for the corn field border to 22% ($n = 454$) for the grassland; this increase was not significant. Independence analysis with the G-test between parasitism and sex was positive. Results were similar in multiple comparisons between habitat, sex and spacing behavior.

Parasitism showed no effect on host reproduction activity. Moreover, active rodents showed more infections (36%) than the inactive ones (23%); these differences were not significant. The results were similar in each season (Table 2). The Kruskal-Wallis test demonstrated no statistical differences between home ranges of infected and uninfected rodents, neither during the fall ($H = 0.437$, $n = 66$) nor during the spring seasons ($H = 1.704$, $n = 24$).

There was no single pattern between host survival and bot fly parasitism. During summer 1986 (Fig. 3) survival was similar for both infected and uninfected animals ($lx = 0.06$ and 0.09 ; $n = 16$ and 44 , respectively; $\chi^2 = 2.8$). During the critical winter period (May to September), uninfected mice survived better ($lx = 0.19$, $n = 107$) than infected ones ($lx = 0.08$, $n =$

TABLE 1. Prevalence of *Rogenhofera bonaerensis* larvae in different host age classes of the pampean grassland mouse.

Season	Host age classes			G*
	Juvenile	Subadult	Adult	
Fall (1986)	19 (36)	25 (137)	27 (103)	0.886 (276)
Spring (1985–1986)	18 (56)		51 (79)	14.405* (135)
Overall	16 (71)	25 (158)	37 (182)	14.062* (411)

* Independence test value; sample size in parentheses.

^b Expressed as %.

* $P < 0.001$.

65, $\chi^2 = 4.25$, $P < 0.05$) (Fig. 4). Winter life expectancy for each group was 2.5 mo for the uninfected mice and 1.9 mo for the parasitized ones.

Prevalence and specificity

Total rodent captures ($n = 607$) included three species of family Cricetidae, *A. azarae* (415), *O. flavescens* (95), and *Calomys laucha* (7). Only 23% ($n = 141$) were parasitized with bot fly larvae; 99% ($n = 140$) in *A. azarae* and 1% in *O. flavescens* ($n = 1$).

DISCUSSION

Subcutaneous localization of bot fly larvae near the tail was high (82%) suggesting no important effect on vital organs and indicating a well adapted host-parasite relationship. Localization of bots on hosts native to the Nearctic is not as uniform (Catts, 1982), but does not greatly differ from our *A. azarae* records.

The seasonal occurrence of *R. bonaerensis* is characterized by its occurrence during two seasons (late spring and fall). This is similar to most other studies (Wecker, 1962; Catts, 1965, 1982; Baird, 1974, 1979; Hensley, 1976) on cuterebrid life cycles.

Despite the lack of association between total population density of the host and prevalence of cuterebrids, two patterns

TABLE 2. Prevalence of *Rogenhofera bonaerensis* larvae across two classes of host reproductive activity.

Season	Reproductive status		G*
	Active	Non-active	
Fall (1986)	31 ^b (35)	21 (281)	1.319 (216)
Spring (1985–1986)	37 (86)	39 (44)	0.001 (130)
Overall	36 (121)	23 (325)	3.606 (446)

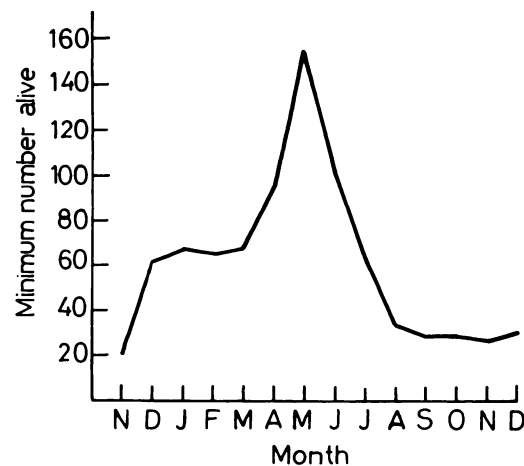
* Independence test value, no statistical differences between groups; sample size in parentheses.

^b Prevalence expressed as %.

have been detected. There are (1) a spring pattern where the association is characterized by a short 2 mo term and by the November synchrony of infection in most animals and (2) the fall pattern where parasite distribution seems to be a normal distribution, without synchrony, and lasts 4 mo (March to June). The spring pattern suggests an eruptive increase in adults which develops in association with changing environmental factors (e.g., day length). Alternatively, a generation overlap could explain the fall pattern as a result of different rates of development on (1) summer pupation, (2) consecutive fall cohorts, or (3) a combination of both.

Spring prevalence of bot fly larvae was almost two fold (1.8:1) when compared with the fall prevalence. During the spring, rodent activity is close to the nest (high reproductive effort, low movement and low density), while in fall an opposite pattern has been recorded (Crespo, 1966; Dalby, 1975). Egg-laying sites close to the host nest site have been found in *Cuterebra buccata* (Beamer, 1950), *C. latifrons* (Catts, 1967), and *C. polita* (Graham and Capelle, 1970). If subsequent studies show a similar oviposition mechanism for *R. bonaerensis*, this would explain the contrasting seasonal prevalences.

The absence of intrapopulation preference is indicated by the independence between parasitism and sex and/or spacing

FIGURE 2. Monthly density of *Akodon azarae* in Argentina.

behavior. Nevertheless, the high percentage of adults and residents infected during the spring could be explained because (1) their survival is higher than the other age classes (Zuleta, 1988), and (2) the proportion of overwintering adults is higher than the recruit classes (Pearson, 1967; Zuleta et al., 1988). During the fall there were no differences in bot fly prevalence between spacing behavior nor rodent age; spacing behavior is similar between age classes, population structure is represented by all age classes and fall survival is similar between them (Dalby, 1975; Zuleta, 1988). This suggests a bot fly strategy more opportunistic than specialist during both seasons.

Most published studies concerning preferences do not result in plausible explanations: Wecker (1962) did not detect preferences by age or sex in *Peromyscus leucopus*, and Hunter et al. (1972) did not find differences between transients and residents of *P. maniculatus*. In contrast Bennett (1972) reported a greater prevalence of bot fly larvae in adult females and immatures of *Tamias striatus*, Boonstra et al. (1980) showed a decrease in prevalence according to age in *Microtus townsendii*, and Catts (1982) believed that the pioneer behavior of male and subadult mice in-

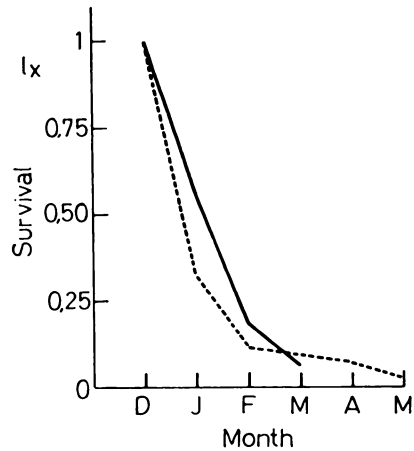


FIGURE 3. Summer survival for bot fly infected (solid line) and uninfected (broken line) *Akodon azarae*. There were no significant differences between curves at $P < 0.05$.

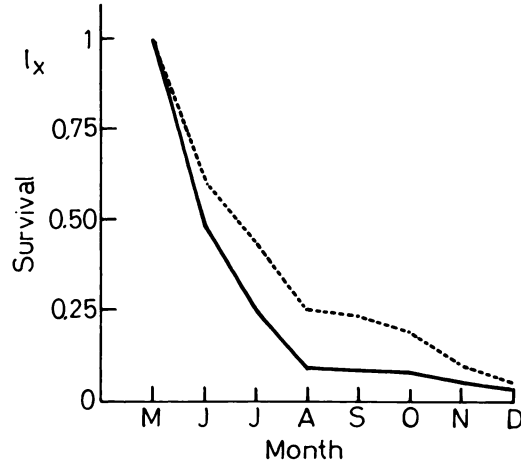


FIGURE 4. Winter survival for bot fly infected (solid line) and uninfected (broken line) *Akodon azarae*. Survival curves are significantly different at $P < 0.05$.

creased their probability for infection with bot flies.

Rogenhofera bonaerensis parasitism could become an additional mortality factor in the pampean grassland mouse population during the winter. The uninfected segment of the host population survives 2.8 times longer than the infected one: the mean expectation for further life is 2.5 mo for the uninfected and 1.9 mo for the infected animals. Detrimental effects on survival have been reported in *M. townsendii* (Boonstra et al., 1980), *M. pennsylvanicus* (Iverson and Turner, 1968) and *Peromyscus* spp. (Wecker, 1962; Hunter et al., 1972). At present, consequences of parasitism are controversial. Boonstra et al. (1980) reported reduced reproduction, depressed survival and a reduction of growth rates of infected rodents. Both Dunaway et al. (1967) and Smith (1978) suggested that infected animals could move about only with great difficulty and were more susceptible to predation. In *M. townsendii* infection with cuterebrids favors a secondary infection with the grey flesh fly (*Wohlfartia vigil*) promoting the death of the host (Boonstra, 1977).

In our study there were no significant differences in survival by sex, age or spacing behavior between infected and unin-

fected mice. Secondary infections have not been recorded and there was no impact on host reproduction. Dalby and Heath (1976) suggested that *A. azarae* has a deficient thermoregulation and this becomes critical during the winter period where (because under this situation) weight loss and a deterioration of physiological condition are common in rodents (Slade et al., 1984; Wolff, 1984). Sealander (1961) found hemoglobin concentration imbalance in infected *P. leucopus*. Reduction in the albumin-to-globulin ratio of parasitized *P. maniculatus* have been reported by Payne et al. (1965). Bennett (1973) detected in the eastern chipmunk (*T. striatus*) that parasitized animals were anemic and had a white blood cell count twice that of the uninfected animals. This evidence supports the hypothesis that fall parasitism appears to be an extra energetic cost becoming critical for winter survival of the pampean grassland mouse.

In both pampean grasslands and agroecosystems, numeric increases of *Calomys musculinus*, *C. laucha* and/or *O. flavescens* have been reported as a result of the removal of *A. azarae* (De Villafañe et al., 1973; Busch, 1987). In addition, habitat stability reductions (De Villafañe et al., 1977; Kravetz, 1978) promote declines in

A. azarae populations. Busch (1987) also found an asymmetric competition by the pampean grassland mouse. This affects the survival, reproduction and habitat use of its sympatric species more than in the opposite sense. This is additional evidence that the pampean grassland mouse is the key species within the cricetid assemblage. *Calomys* spp. represents the r-selected species (low survival, high reproductive effort, small size, simple sociability), *A. azarae* is a K-selected one (high survival, low reproductive effort, complex sociability), and *O. flavescens* has an intermediate life-history strategy (De Villafañe et al., 1977; Zuleta, 1989). Also, *R. bonaerensis* demonstrated strong host specificity for the pampean grassland mouse. These results suggest the coevolutionary adaptative hypothesis (May and Anderson, 1983) as a plausible explanation; the pampean grassland mouse is a better alternative for parasite perpetuation than other members of the cricetid assemblage.

ACKNOWLEDGMENTS

We thank F. Kravetz, C. Bernstein, A. Kuris, O. Pearson, S. Coscarón and L. Venturini for criticisms and suggestions on earlier drafts of the manuscript. M. Busch, R. Feldman, M. Bellocq and an anonymous reviewer contributed additional helpful comments. D. Bilenca's assistance in field work had been essential. We are indebted to the people of Diego Gaynor for their accommodations and kindness, especially to the Mazzanti family. S. Nieto and J. Rabinovich helped us with the English revision. Financial support was provided by the Consejo Nacional de Investigaciones Científicas y Tecnológicas (CONICET-Argentina).

LITERATURE CITED

- BAIRD, C. R. 1974. Field behavior and seasonal activity of the rodent bot fly, *Cuterebra tenebrosa*, in central Washington (Diptera: Cuterebridae). Great Basin Naturalist 34: 247-253.
- . 1979. Incidence of infection and host specificity of *Cuterebra tenebrosa* in bushy-tailed wood rats (*Neotoma cinerea*) from central Washington. The Journal of Parasitology 65: 639-644.
- BEAMER, R. H. 1950. An observation on the egg-laying of *Cuterebra buccata* Fabr. in nature. Journal of The Kansas Entomological Society 23: 16.
- BENNETT, G. 1972. Further studies on the chipmunk warble, *Cuterebra emasculator* (Diptera: Cuterebridae). Canadian Journal of Zoology 50: 861-864.
- . 1973. Some effects of *Cuterebra emasculator* Fitch (Diptera: Cuterebridae) on the blood and activity of its host, the eastern chipmunk. Journal of Wildlife Diseases 9: 85-93.
- BERG, C. 1876. Naturgeschichte der *Rogenhoferia grandis* einer Fliege aus der Familie der Oestriden. Entomologische Stettin Zeitung 37: 268-272.
- BLAIR, W. F. 1940. Home ranges and populations of the meadow vole in southern Michigan. The Journal of Wildlife Management 4: 149-161.
- BOONSTRA, R. 1977. Effect of the parasite *Wohlfahrtia vigil* on *Microtus townsendii* populations. Canadian Journal of Zoology 55: 1057-1060.
- , C. J. KREBS, AND T. D. BEACHAM. 1980. Impact of botfly parasitism on *Microtus townsendii* populations. Canadian Journal of Zoology 58: 1683-1692.
- BROWN, J. L., AND G. H. ORIAN. 1970. Spacing patterns in mobile animals. Annual Review of Ecology and Systematics 1: 239-262.
- BUSCH, M. 1987. Competencia interespecífica en roedores silvestres. Ph.D. Thesis. Universidad de Buenos Aires, Buenos Aires, Argentina, 126 pp.
- CATTS, E. P. 1965. Host-parasite interrelationships in rodent botfly infections. Transactions of the 30th North American Wildlife and Natural Resources Conference 13: 184-196.
- . 1967. Biology of a California rodent bot fly *Cuterebra latifrons* Coquillett (Diptera: Cuterebridae). Journal of Medical Entomology 4: 87-101.
- . 1982. Biology of New World botflies: Cuterebridae. Annual Review of Entomology 27: 313-338.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, New York, New York, 234 pp.
- CRESPO, J. A. 1966. Ecología de una comunidad de roedores silvestres en el Partido de Rojas, Provincia de Buenos Aires. Revista del Museo Argentino de Ciencias Naturales, Ecología 1: 79-134.
- DALBY, P. 1975. Biology of pampa rodents. Balcarce Area, Argentina. Publications of the Museum of Michigan State University, Biological Series 5: 149-272.
- , AND A. G. HEATH. 1976. Oxygen consumption and body temperature of the Argentine field mouse, *Akodon azarae*, in relation to ambient temperature. Journal of Thermal Biology 1: 177-179.
- DEL PONTE, E. 1939. Revisión de los Oestridae argentinos. Physis 17: 525-534.
- . 1959. Diptera Cuterebridae. Primeras Jornadas Entomopidemiológicas Argentinas 2: 575.

- DE VILLAFANE, G. 1981. Reproducción y crecimiento de *Akodon azarae azarae* (Fisher, 1829). *Historia Natural* 1: 193–204.
- , F. O. KRAVETZ, M. J. PIANTRANIDA, AND J. A. CRESPO. 1973. Dominancia, densidad e invasión en una comunidad de roedores de la localidad de Pergamino (Provincia de Buenos Aires). *Physis* 32: 47–59.
- , F. O. KRAVETZ, O. DONADIO, R. PERCICH, L. KNECHER, M. P. TORRES, AND N. FERNANDEZ. 1977. Dinámica de las comunidades de roedores en agroecosistemas pampásicos. *Medicina* (Buenos Aires) 37: 128–140.
- DUNAWAY, P. B., J. A. PAYNE, L. L. LEWIS, AND J. D. STORY. 1967. Incidence and effects of *Cuterebra* in *Peromyscus*. *Journal of Mammalogy* 43: 38–51.
- GRAHAM, C. L., AND K. J. CAPELLE. 1970. Redescription of *Cuterebra polita* (Diptera: Cuterebridae) with notes on its taxonomy and biology. *Annals of the Entomological Society of America* 63: 1569–1573.
- GROSS, A. J., AND V. A. CLARK. 1975. Survival distributions: Reliability applications in the biomedical sciences. John Wiley and Sons, New York, New York, 331 pp.
- HENSLEY, M. S. 1976. Prevalence of cuterebrid parasitism among woodmice in Virginia. *Journal of Wildlife Diseases* 12: 172–179.
- HOLLANDER, M., AND D. A. WOLFE. 1973. Non-parametric statistical methods. John Wiley and Sons, New York, New York, 503 pp.
- HUNTER, D. M., R. M. ADLEIR, AND J. M. WEBSTER. 1972. Studies on the ecology of cuterebrid parasitism in deer mice. *Canadian Journal of Zoology* 50: 25–29.
- IVERSON, S. L., AND B. A. TURNER. 1968. The effect of *Cuterebra* sp. on weight, survival and reproduction in *Microtus pennsylvanicus*. *Manitoba Entomology* 2: 70–75.
- KRAVETZ, F. O. 1978. Ecología de las comunidades de roedores involucrados en la Fiebre Hemorrágica Argentina. Ph.D. Thesis. Universidad de Buenos Aires, Buenos Aires, Argentina, 309 pp.
- KREBS, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs* 36: 239–272.
- LYNCH ARRIBALZAGA, E. 1881. Diptera. Informe Oficial de la Comisión Científica agregada al Estado Mayor General de la Expedición al Río Negro (Patagonia), realizada en los meses de abril, mayo y junio; bajo los órdenes del General J. A. Roca. Buenos Aires, Argentina, 89 pp.
- MAY, R., AND R. M. ANDERSON. 1983. Parasite-host coevolution. In *Coevolution*, D. J. Futuyuma and M. Slatkin (eds.). Sinauer Associates Inc., Boston, Massachusetts, pp. 186–206.
- PAYNE, J. A., P. B. DUNAWAY, G. D. MARTIN, AND J. D. STORY. 1965. Effects of *Cuterebra angustifrons* on plasma proteins of *Peromyscus maniculatus*. *The Journal of Parasitology* 51: 1004–1008.
- PEARSON, O. P. 1967. La estructura por edades y la dinámica reproductiva de una población de roedores de campo, *Akodon azarae*. *Physis* 27: 53–58.
- PYKE, D. A., AND J. N. THOMPSON. 1986. Statistical analysis of survival and removal rate experiments. *Ecology* 67: 240–245.
- SLADE, N., J. SAUER, AND G. GLASS. 1984. Seasonal variation in field-determined growth rates of the hispid cotton rat (*Sigmodon hispidus*). *Journal of Mammalogy* 65: 263–270.
- SEALANDER, J. A. 1961. Haematological values in deer mice in relation to bot fly infection. *Journal of Mammalogy* 42: 57–60.
- SMITH, D. H. 1978. Effects of the bot fly (*Cuterebra*) parasitism on activity patterns of *Peromyscus maniculatus* in the laboratory. *Journal of Wildlife Diseases* 14: 28–39.
- SOKAL, R. R., AND F. J. ROHLF. 1979. *Biometria: Principios y métodos estadísticos en la investigación biológica*. H. Blume, Madrid, España, 832 pp.
- STICKEL, L. F. 1954. A comparison of certain methods of measuring ranges of small mammals. *Journal of Mammalogy* 35: 1–15.
- WECKER, S. C. 1962. The effects of bot fly parasitism on a local population of the white-footed mouse. *Ecology* 43: 561–565.
- WOLFF, J. 1984. Overwintering behavioral strategies in taiga voles (*Microtus xanthognathus*). In *Winter ecology of small mammals*. Special Publication of the Carnegie Museum of Natural History 10, Pittsburgh, Pennsylvania, pp. 315–318.
- ZULETA, G. 1984. Usos del espacio por *Akodon azarae* (Rodentia, Cricetidae), en agroecosistemas. *Actas de las VII Jornadas Argentinas de Zoología* 7: 283.
- . 1989. Estrategias de historia de vida en el ratón del pastizal pampeano, *Akodon azarae*. Ph.D. Thesis. Universidad de Buenos Aires, Buenos Aires, Argentina, 256 pp.
- , F. O. KRAVETZ, M. BUSCH, AND R. E. PERCICH. 1988. Dinámica poblacional del ratón del pastizal pampeano (*Akodon azarae*) en ecosistemas agrarios. *Revista Chilena de Historia Natural* 61: 231–244.

Received for publication 12 August 1988.