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Cuterebrid Parasitism (*Rogenhofera bonaerensis*) on the Shrubland Mouse (*Akodon molinae*), in Argentina

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ABSTRACT: We evaluated the influence of temperature, rainfall, and host relative abundance on Rogenhofera bonaerensis (Diptera, Cuterebridae) parasitism prevalence in shrubland mouse (Akodon molinae) populations in central Argentina, from February 1983 to December 1987. Parasitism did not vary significantly with host age: juvenile-subadults (32%), adults (26%), and old adults (29%). Females were more frequently parasitized (36%) than were males (20%). There was no correlation between parasitism and reproductive activity. Infested hosts were recorded most commonly in summer (January to March, 19%), and in fall (April to June, 30%). During the dry season, July through November, cuterebrid parasitism averaged only 3%. The monthly prevalence of parasitism throughout the year was not associated either with monthly precipitation nor with mean monthly temperature at the time of sampling. But a 2 to 3 month time-lag effect of both climatic variables on parasitism was recorded. Bot fly prevalence was correlated to an index of host density. We propose climate and host availability as important factors affecting bot fly parasitism in the semiarid shrubland of central Argentina.

Key words: Host-parasite relationship, prevalence, seasonality, climate, Rogenhofera bonaerensis, Akodon molinae, Argentina.

Bot fly larvae of the family Cuterebridae are subcutaneous parasites of mammals in the New World (Sabrovsky, 1986); there are many studies on the impact of these flies on Nearctic rodents (Catts, 1982). But very little is known about the influence of climate and host availability on parasite performance (Baird, 1974; Meyer and Bock, 1980), especially in the Neotropic region (Guimarães et al., 1983); however, recent studies on host-parasite relationships have been reported by Bossi and Bergallo (1990) and Zuleta and Vignau (1990).

In Pampean grasslands of Argentina, the most abundant mouse, Akodon azarae (Rodentia: Cricetidae), is parasitized by Rogenhofera bonaerensis (Diptera: Cuterebridae) (Zuleta and Vignau, 1990). This same bot fly also parasitize the most common mouse, A. molinae, of central Argentinean shrublands, in spite of marked climatic and productivity differences between these two ecosystems (Cabrera and Willink, 1980). Shrublands are semiarid and highly seasonal with an extended dry season, whereas Pampean grasslands are among the world's most productive grasslands. Secondary productivity and mouse availability change dramatically. and parasite populations should respond accordingly. Our objective was to determine whether monthly prevalence of R. bonaerensis varied with host availability or climate.

The study area was a 4 km² shrubby habitat near Donovan (33°20'S, 66°21'W), San Luis Province, Argentina. The climate is semiarid with a mean annual precipitation (1961 to 1987 records) of 493 mm. Mean monthly temperatures (1961 to 1987 records) ranged from 8.9 C in July to 24 C in January. Climatic data used in analvses were obtained from a meteorological station 2 km from our study area that was maintained by the Department of Statistical Economy (San Luis, Argentina). Elevations average 750 m. The habitat is composed of 60% herbaceous species; dominant tree species are carob (Prosopis flexuosa) and chañar (Geoffrea decorticans).

To estimate the parasitism seasonality, Akodon molinae populations were monitored by monthly removal trapping from February 1983 to December 1987, except during 1985 when traps were set only between January and May. The sampling technique involved 4 days of removal trapping for each period. Usually, two traplines were located randomly at different sites within the study area each month, and at least 500 m apart to avoid dispersal effects due to the removal. Stations were set on lines of 11, 49, and 40 traps during 1983, 1984 to 1985, and 1986 to 1987, respectively, with 5-m spacing between stations on all traplines. Each station was represented by a single trap. We used commercial snap-traps between 1983 and 1985, and home-made Sherman-like live traps during 1986 and 1987. All lived-trapped animals were killed by exposure to ethyl ether. Traps were baited with peanut butter and bovine fat, opened at sunset, and examined at sunrise. Overall trapping effort was 13,019 trap-nights between 1983 and 1987.

Population size was estimated as the number of mice captured per 100 trapnights. For each captured animal we recorded trap location, species, sex, reproductive condition, total length, tail length, and evidence of cuterebrid parasitism by presence of third-instar larvae (L3). Reproductive condition was estimated as active (perforate females; scrotal males) or non-active (imperforate females; testes abdominal). The following age classes were defined according to the eye lens weight (Lord, 1959): juvenile-subadults (<0.600 g), adults (0.600 to 0.849 g), and old adults (\geq 0.850 g).

Simple and multiple independence G analyses (Sokal and Rohlf, 1981) were used to determine relationships between parasitism prevalence, and age, sex, and reproductive condition. Multiple linear regressions were performed to identify the relevant variables associated with the monthly parasitism prevalence (MPP) as the single dependent variable; independent variables were monthly host relative abundance (ABUN), monthly total precipitation (RAIN), and monthly mean temperature (TEMP). To evaluate the relationship between ABUN and climatic variables, ABUN also was a dependent variable in the multiple regression analyses. We additionally completed simple regression models to control covariation between rain and temperature. To evaluate whether there was a time-lag effect of climate on parasitism or host abundance, we also ran cross-correlation time series models to identify the proper time delay. We evaluated series of RAIN and TEMP from one (RAIN-1; TEMP-1) to six months (RAIN-6; TEMP-6) previous to the current estimated MPP and ABUN. All regressions and time series analyses were performed from the SYSTAT software (Wilkinson, 1988). Percent data were subjected to an arcsin of the square-root transformation (Zar, 1984) prior to analysis. The level of probability identified as statistically significant was P < 0.05.

Identification of bot flies was based upon the description of adults and larvae by Del Ponte (1939) and Vignau and Zuleta (1991), respectively. Twenty-five mature L3 were removed from hosts, using ethyl ether to induce the parasites to leave (Zuleta, 1989). Under laboratory conditions, those emerging as adults (n = 2 females and 2 males)were used for taxonomic identification. Voucher specimens are deposited in the collection of the Department of Parasitology, Faculty of Veterinary Sciences, University of La Plata, La Plata, Argentina. Although no accession numbers were given, voucher specimens can be requested by mentioning the published source.

Most parasitized hosts (Table 1) were trapped in summer (January to March) (7 of 36 mice) and in fall (April to June) (38 to 128). Occasionally, parasitized hosts occurred in winter (July to September) (2 of 76) or in spring (October to December) (3) of 88). No infested animals were caught during August and October, and only one parasitized mouse was caught during each of July, September and December. Infestation prevalence was significantly higher in January through June than in July through December (G = 42.580, P <0.0001, n = 328). January through June will be referred to as the high-infestation season (HIS).

During the HIS, parasite prevalence did

TABLE 1. Monthly prevalence (MPP) of Rogenhofera bonaerensis in Akodon molinae from Donovan, Argentina (1983 to 1987). Numbers in parenthesis indicate sample size of animals trapped. Host abundance (ABUN) is also indicated as the number of mice captured per 100 trap-nights in 1987, when all months were represented in captures.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
МРР	16.7 (6)	182 (11)	21.0 (19)	32.4 (37)	33.3 (42)	22.4 (49)	5.3 (19)	0 (21)	2.8 (36)	0 (38)	8.3 (24)	3.8 (26)
ABUN	0.9	0.3	1.9	8.9	6.8	3.9	2.5	2.4	2.2	2.0	2.1	2.5

not vary significantly by age class: adults (25.4%) < old adults (28.6%) < juvenilesubadults (31.7%) (G = 0.569, n = 126). The percentage of infested mice differed significantly between sexes: 35.8% in females and 20.0% in males (G = 4.991, P < 0.05, n = 162). Adult females were the most commonly parasitized group (40.7%), n = 74). When females and males were combined, there was no significant difference in parasite prevalence between reproductively active mice (26.9%), and nonactive ones (27.8%) (G = 0.014, n = 149). But in a multiple comparison, there was no statistical difference between parasite prevalence and combined categories of age classes and reproductive condition in both females (G = 2.079, n = 72) and males (G= 0.402, n = 82).

Based on a simple linear regression model (F-ANOVA = 6.331, P < 0.05, df = 10, r = 0.39) MPP was associated with the concurrent ABUN. Using multiple regression analyses, we found that neither MPP nor ABUN, as dependent variables, were associated with the RAIN and TEMP at the time of sampling. However, we found a 2 to 3 mo time-lag effect of RAIN and TEMP on both biological variables. According to the cross-correlation time series models, MPP was statistically associated with TEMP-2 (Student's t = 3.084, P <0.02, df: 8, r = 0.74), TEMP-3 (t = 3.234, P < 0.02, df: 7, r = 0.77), and RAIN-3 (t = 2.745, P < 0.05, df: 7, r = 0.72). In turn, ABUN was only associated with RAIN-3 (t = 3.698, P < 0.02, df: 7, r = 0.76).

Differences in trappability among individuals may occur when using both removal (snap) and non-removal (live) trapping techniques (Boonstra and Rood, 1984; Galindo-Leal, 1990). However, these effects were unlikely in our study because we also removed all live-trapped animals. In fact, parasitism did not change according to the trap type: 15.5% (n = 124) and 15.2% (n = 204) in snap and Sherman-like traps, respectively.

From our results, Rogenhofera bonaerensis parasitism did not appear related to reproductive activity of A. molinae individuals. Additionally, parasitism showed no strong specificity for any host population component, but there was a higher prevalence in adult females. Host populations typically occur at very low densities in semiarid shrublands (Brigada et al., 1984). Under this condition, the host-parasite encounter probability is also low across most host microhabitats. Thus, we expected that bot flies deposited their eggs near host nests as has been observed in several cuterebrid species (Catts, 1967; Baird, 1975). This could explain the higher prevalence on adult females.

Rogenhofera bonaerensis populations showed an uninterrupted infestation period (HIS: summer to fall) when parasitizing shrubland mouse populations. During this period they reached peak infestations in April, May, and June (Table 1). Two possible factors, climate and host availability, might be responsible for the seasonal parasitism.

To explain how climate could affect this particular host-parasite association, we propose the following parasite life cycle based on the generalized life history of a cuterebrid bot fly (Catts, 1982) and on the available information for R. bonaerensis

(Zuleta, 1989; Zuleta and Vignau, 1990): a free-living period, from adult emergence to entry into the host, lasting 2 to 3 wk; an endoparasitic period in the host, from the first to third instar larvae, lasting 2 to 3 mo; and a pupation period lasting 6 to 9 mo.

Cuterebrid life cycles are strongly influenced by climatic conditions (Catts, 1967; Hunter and Webster, 1974; Baird, 1974; Meyer and Bock, 1980; Catts, 1982); cuterebrids also are geographically restricted to the tropics and the temperate regions (Guimarães et al., 1983; Sabrovsky, 1986). In central Argentina, since shrublands are characterized by strong seasonality, we predict that climate severely affected parasite performance.

During the endoparasitic period, the direct environment for cuterebrid larvae is the host tissue. So, effects of contemporary weather conditions on MPP probably are minimal. This may explain why we did not find association between MPP and the current climate. However, climate probably affects the parasite outside of the host (free-living and pupation ones). We found that MPP was positively correlated with the climatic variables of the previous 2 to 3 mo. This time-lag also was synchronous with the wet season from November to March. One reason for peak L3 infestation in mice in April, May, and June is that adult bot flies probably reached their peaks of abundance (and laid most eggs) in January, February, and March, when climatic conditions were the most appropriate: warm and humid.

We suggest that cold and dry conditions could be limiting factors for adult emergence, egg development period, and resultant L3 parasitism, whereas humid and warm conditions promote peak infestation rates in shrubland mouse populations.

The relationship between density of hosts and fraction of hosts infested by parasites is key to the basic understanding of the biology of host-parasite systems. Studies analyzing patterns of parasitism and the type of density dependence have received considerable attention recently (May & Hassell, 1988). In Argentina, R. bonaerensis populations have different patterns of parasitism between two of its host species, Akodon molinae and A. azarae. In San Luis shrublands, bot fly prevalence was correlated to an index of host density (this study), whereas in Pampean grasslands it was not (Zuleta and Vignau, 1990). However, that variation also must be related to differences in ecosystem productivity (Cabrera and Willink, 1980). Reported host abundances in the pampas (Zuleta, 1989) were four to seven times higher than in our locality. So, as host availability changes drastically, parasite populations should respond accordingly.

We postulate a strong influence of climate on host availability. Climate and host availability could be mutually related when analyzing their influence on parasite life history. We estimated a 3-mo time-lag effect of climate on ABUN. This supports the idea that the long dry season could be a limiting factor on host availability. As the influence involved only RAIN, the effect was less drastic than in MPP, but strong enough to reinforce the climatic hypothesis discussed above. Therefore, the shrubland's host abundance may represent a secondary limiting factor, climate being the primary one for both parasite and host species.

Shrubland mice begin to breed in September and October (Brigada et al., 1984), under very low densities. Perhaps, these overwintered individuals do not survive the following summer, when the mice born in spring replace them, thus maintaining low-densities. In January, February, and March, newborns probably are infested early but not trapped until reaching the juvenile-subadult stage, presumably in the fall when A. molinae populations reach their peak and also the peak MPP is recorded. Therefore, the summer time offers the optimal conditions for parasitism infestation: wet, warmer weather and high host availability.

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