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Neobellieria citellivora

Gail R. Michener


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LETHAL MYIASIS OF RICHARDSON'S GROUND SQUIRRELS BY THE SARCOPHAGID FLY *NEOBELLIERIA CITELLIVORA*

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Larvae of the sarcophagid fly *Neobellieria* (formerly = *Sarcophaga*) *citellivora* caused lethal cutaneous myiasis in Richardson's ground squirrels from late June through September in southern Alberta, Canada. Of squirrels resident in mid-June during the 3-year study, 8.6% of 348 juveniles eventually were parasitized by *N. citellivora*, whereas only 1.0% of 197 adults were parasitized. Among juveniles, 13.0% of 154 males and 5.2% of 194 females were parasitized. Age- and sex-specific differences in time of entry into hibernation accounted for this differential vulnerability of squirrels to parasitism. Squirrels usually were infested with >80 larvae, and frequently with >200 larvae, resulting in massive tissue damage and subsequent death.

Key words: *Spermophilus*, parasites, *Neobellieria citellivora*, Canada

Although the majority of parasitic species of sarcophagid flies select insects and other arthropods as their hosts, some species larviposit on live mammals (Shewell, 1987). *Neobellieria* (formerly = *Sarcophaga*) *citellivora* was first described by Shewell (1950) from adults reared from larvae infesting Columbian ground squirrels (*Spermophilus columbianus*) in British Columbia, Canada. Except for my observation of myiasis by *N. citellivora* in two juvenile Richardson's ground squirrels (*S. richardsonii*) from the foothills of southern Alberta (Michener, 1979), no information on host-parasite relationships is available for this larviparous fly. Here I report that infestations by *N. citellivora* cause fatal cutaneous myiasis, and that infestations are more common on juvenile than adult Richardson's ground squirrels.

**Study Area and Methods**

The incidence of myiasis was determined for two populations of Richardson's ground squirrels located, respectively, 8 km E and 5 km SE Picture Butte in southern Alberta, Canada. During 8 years (1979–1986) of intensive study of the first population (Michener and Locklear, 1990a, 1990b), I detected no myiasis. Due to an anticipated change in land management practice that resulted in destruction of this population in 1986, I removed squirrels in both 1985 and 1986 for release at the second site, 3 km away. Although Richardson's ground squirrels had inhabited the 1.4-ha release site previously, none were resident from 1979 to 1984 because the vegetation had grown too tall to be suitable for these squirrels. By a combination of burning and grazing, the site was returned to habitat appropriate for Richardson's ground squirrels. I released seven females (six with litters) in 1985 and an additional seven females (four with litters) in 1986. The newly founded population increased rapidly. The numbers of adults (≥1-year-old) that emerged from hibernation over the ensuing years were 31 females and 2 males in 1987, 55 females and 16 males in 1988, 101 females and 28 males in 1989, and 193 females and 62 males in 1990. As a result of badger (*Taxidea taxus*) predation on hibernating squirrels in 1990–1991, the population declined to 103 females and 32 males in spring of 1991.

All squirrels were uniquely identified with a numbered metal tag in each ear. All adults and a selection of juveniles also were given a unique dye mark that permitted individuals to be iden-
tified from a distance (Michener, 1992). At the newly founded site, dates of emergence of adults from hibernation and of litters from the natal burrow and dates of emergence into hibernation were determined by almost daily observation throughout the active season. To assess sexual and seasonal patterns in prevalence of parasitism of juvenile Richardson's ground squirrels, I used live-trapping and observation data to determine the minimum number of juveniles in the aboveground population at half-monthly intervals from mid-June onwards. Prevalence was estimated only for those portions of the study site (0.55 ha in 1989, 0.30 ha in 1990, 0.76 ha in 1991) on which I was likely to detect most occurrences of myiasis because I conducted visual inspection of resident juveniles, using binoculars, almost daily.

Most (28/30) live squirrels with myiasis were killed immediately, usually with an overdose of sodium pentobarbital or by carbon dioxide inhalation. A sample of larvae was collected for subsequent determination of the proportions of first, second, and third instars. Larvae were assigned to instar based on the appearance of the cephalopharyngeal skeleton and the posterior spiracles (Knippling, 1939). The total number of larval *N. citellivora* per host was assessed for some squirrels either by removal of all visible larvae from fresh carcasses and live squirrels, by rearing of larvae on the host carcass to obtain pupae and adult flies, or by removal of all larvae from alcohol-preserved carcasses. These counts give minimum estimates of the total larval burden on host squirrels as small live larvae may not have been detected for removal, some larval mortality probably occurred during rearing to pupation, and some mature larvae may have already migrated off-hosts. Total counts of larvae were made only for squirrels that were found alive.

**Results and Discussion**

No myiasis was detected in the newly founded population of Richardson’s ground squirrels in 1987 or 1988, but 18 squirrels infested with *N. citellivora* were found in 1989, 11 in 1990, and 7 in 1991. Because the released Richardson’s ground squirrels that founded the study population were healthy, because the release site had not been inhabited by ground squirrels for >5 years, and because no myiasis was detected in the 2 years following releases of squirrels, adult *N. citellivora* must have arrived in the newly founded population from elsewhere in 1989. Thereafter, adult flies could have emerged from pupae that overwintered on the study site.

Of the 36 Richardson’s ground squirrels known to have been parasitized by *N. citellivora*, 6 were found dead, 11 were moribund and captured by hand, 12 exhibited obvious signs of myiasis but were sufficiently active that they could not be caught by hand so were livetrapped, and 7 appeared healthy but infestation with maggots was detected when the squirrel was trapped. In 1989, I attempted to treat two squirrels under anesthesia by removing all visible larvae, then suturing the wounds caused by the fly larvae. One squirrel was immediately released, but when recaptured 2 days later large larvae were visible in the wound, indicating that I failed to remove all larvae during treatment. The second squirrel received a topical application of the antiparasitic ivermectin (Ivomec, Merck Frosst Canada, Inc.) and was released 2 days after treatment. When inspected 2 and 3 days after release, the lesion was healing and free of larvae. However, the lesion on this squirrel was reinfested with *N. citellivora* larvae 5 days after release. I subsequently killed both of these treated squirrels.

Over the 3-year study period, I found 1 adult male, 1 adult female, 10 juvenile females, and 24 juvenile male squirrels parasitized by *N. citellivora*; 30 of the 34 juveniles resided within the regularly inspected portions of the site. Of Richardson’s ground squirrels resident in mid-June each year and visually inspected at almost daily intervals until emergence, 8.6% of 348 juveniles eventually were parasitized by *N. citellivora*, whereas only 1.0% of 197 adults were parasitized ($\chi^2$ with Yates' correction = 11.83, $P < 0.001$). I attribute the differential prevalence of parasitism among age and sex classes to differences in the timing of the active season. The mean ± SD dates of emergence in 1989 were 26 June ± 14 days
dates of immurgence were 28 May ± 14 days for 4 adult male squirrels, 21 June ± 12 days for 64 adult females, 4 August ± 9 days for 46 juvenile females, and 7 October ± 14 days for 13 juvenile males, whereas the range of infestation dates was 7 July to 27 August.

Parasitism by *N. citellivora* was significantly more prevalent among juvenile males than juvenile females (Table 1); of juveniles present in mid-June, 13.0% of 154 males and 5.2% of 194 females eventually were parasitized by *N. citellivora* ($\chi^2$ with Yates’ correction = 5.73, $P < 0.05$). This sexual trend in prevalence primarily was attributable to the longer active season of juvenile males, such that many males but few females were available as hosts from late August onwards (Table 1). The proportions of juvenile males and females parasitized from late June through early August, before most females immersed into hibernation, did not differ significantly ($\chi^2$ with Yates’ correction = 1.51, $P > 0.20$).

Prevalence of parasitism was low in late July then increased in August, perhaps indicating that there were at least two generations of flies, an over-wintered generation responsible for the first infestations of the season and a summer generation responsible for infestations in August and September. Further evidence for a summer generation is provided by the observation that, of squirrels from which adult flies were reared, 15 of 16 squirrels parasitized from June through early August produced adults that season compared with only 1 of 6 squirrels parasitized from late August through early September. Flies reared on the other six squirrels did not eclose until after 3–4 months of pupal diapause at room temperature; presumably these pupae would have overwintered under natural conditions.

Richardson’s ground squirrels usually were infested with >80 larval *N. citellivora*, and most ($15/21 = 71\%$) had total burdens of ≥200 larvae (Table 2). Fecondity of *N. citellivora* is not known. Because most sarcophagids larviposit <100 larvae, and com-
monly <50, at one time (Ives, 1991; Knipling, 1936; So and Dudgeon, 1989), the large numbers of larvae parasitizing Richardson's ground squirrels probably result from multiple strikes on the host. The distribution of larval sizes and instars determined for larvae removed from the three alcohol-preserved squirrels suggests that multiple strikes do occur. On one carcass, third-instar larvae exhibited a bimodal distribution in length, with 57% of 232 larvae measuring 10.7–15.3 mm (mean ± SD = 12.8 ± 0.9 mm) and the remaining 43% measuring 5.0–10.5 mm (8.2 ± 1.0 mm). This squirrel also had 115 second-instar larvae that were significantly shorter in length (6.3 ± 0.9 mm) than the shorter group of third-instar larvae (t = 14.0, P < 0.001). Presumably this moribund squirrel had been struck at least three times, with the first population of larvae nearly mature and migratory, the second population recently molted to third instar, and the third population late in the second instar. On another carcass, the larvae fell into two distinct groups, 57 small second-instar larvae (4.4 ± 0.6 mm) and 32 large third-instar larvae (10.9 ± 1.4 mm, t = 29.5, P < 0.001), again suggestive of two separate larvipositions. On the third carcass, the second- and third-instar larvae overlapped in size but still differed significantly in length (6.6 ± 0.5 mm for 93 second-instar larvae compared with 9.7 ± 1.4 mm for 184 third-instar larvae, t = 21.1, P < 0.01), possibly because they resulted from two separate larvipositions.

The large number of larval *N. citellivora* infesting Richardson’s ground squirrels resulted in massive tissue damage. The magnitude of tissue damage and the condition of the squirrel at capture were correlated with duration of the infestation, as indicated by larval development (Table 2). Active squirrels were infested with first-instar and small second-instar larvae but no third-instar larvae, whereas moribund squirrels had few (≤10%) first-instar larvae, many second-instar larvae, and a substantial burden (>25%) of third-instar larvae. Squirrels on which the majority of larvae were at the second or third instar experienced loss of mass and exhibited tissue damage extending over areas as large as 45 by 55 mm (Table 2). The most extreme decline in mass recorded was for a juvenile male that lost 31.5% of its mass in the 11-day period between the last capture when uninfested and its discovery in a weakened, but not yet

### Table 1

Prevalence of cutaneous myiasis by Neobellieria citellivora in juvenile Richardson’s ground squirrels near Picture Butte, Alberta. Data are presented as the number of parasitized squirrels found during half-monthly intervals, with the minimum number of squirrels present in that half month in parentheses. Prevalence was determined for juveniles resident from late June onwards within a 0.55-ha area in 1989, a 0.30-ha area in 1990, and a 0.76-ha area in 1991. Mean dates of emergence of litters from the natal burrows were 16 May 1989, 1 May 1990, and 6 May 1991.

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<td>Males</td>
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<td>0 (74)</td>
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<td>1 (62)</td>
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<td>Early August</td>
<td>2 (36)</td>
<td>4 (35)</td>
<td>1 (20)</td>
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<td>Late August</td>
<td>2 (16)</td>
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<td>Total prevalence</td>
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<td>8 (55)</td>
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<td>9.5%</td>
<td>14.5%</td>
<td>3.2%</td>
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TABLE 2.—Proportions of larval instars and burden of larval Neobellieria citellivora on infested Richardson’s ground squirrels near Picture Butte, Alberta. Squirrels are grouped according to their condition on capture: active squirrels were captured during regular census trapping; visibly infested squirrels were selectively trapped; moribund squirrels were captured by hand. A sample of larvae (N_a) was preserved immediately to assess the proportions of first-, second-, and third-instar larvae. Maximum diameter of the subdermal area infested with larvae was measured on some squirrels. For squirrels that recently had been captured prior to infestation, the change in mass and the interval over which this change occurred are given. Methods of assessing total larval burden were: V = removal of all visible larvae from fresh carcass or live animal; R = larvae reared to pupation on carcass (samples removed to assess instars included in total burden); P = removal of all visible larvae from alcohol-preserved carcass. Year of infestation and sex are indicated for each host.

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* Interval between previous capture when healthy and final capture when myiasis was apparent. The day during this interval on which larviposition occurred was not known for any squirrel.

* Same individual; this squirrel was released following removal of 239 larvae, but 7 days later it was reinfested with 258 new larvae.

† Adults; all others were juveniles.

* Eye infested.

† This squirrel seemed to have scraped off larvae (see text).

* No initial sample collected.
moribund, condition. For ethical reasons, I did not observe the progress of myiasis on still-living hosts. However, observation of the condition of wounds on squirrels at different stages of myiasis when captured permits a general description. Initially, the larvae created one to four small (2 mm) circular cutaneous lesions, characterized by smooth moist edges, fluid drainage onto adjacent fur, and absence of scabbing. As larvae grew and extended the subdermal area in which they were feeding, the number and size of cutaneous lesions increased, adjacent lesions coalesced, and the surrounding skin became necrotic and denuded. On moribund squirrels, the resultant gaping wound was as large as 25 by 30 mm. The extent of subdermal damage, which exceeded that of the damaged and necrotic skin, was evident externally as the area over which the skin was abruptly elevated from the underlying muscle. Extensive fluid drainage, caudal and lateral to the infested area, resulted in darkened matted fur to which soil adhered. For two squirrels that were wearing temperature-transmitting radio collars at the time of infestation, normal body-surface temperatures were 37.0 and 37.7°C (based on twice-daily assessment for 5 days when the squirrels were in their sleeping burrows). However, temperature abruptly increased to 39.5°C for 2 days preceding the underground death of the first animal and to 39.5°C for 2.5 days preceding capture of the other squirrel when it was noted to have a 20-mm lesion containing many second- and some third-instar larvae. Based on the observed tissue damage on live squirrels, the moribund condition of 31% of the 36 parasitized squirrels, the known underground death of a radiotelemetered squirrel, and the discovery above ground of five carcasses infested with third-instar *N. citellivora*, I judged that death would be the inevitable consequence of myiasis by *N. citellivora* in Richardson's ground squirrels.

In addition to the tissue damage caused by larval *N. citellivora*, some moribund squirrels also were infested with larvae of the sarcophagid *Liopygia argyrostoma* and the calliphorids *Calliphora coloradensis* and *Phormia regina*, necrophagous dipters that presumably were attracted to the wound created by the *N. citellivora*. No cuterebrid were found on any squirrels in the population.

Site of initial infestation could be determined for 33 squirrels. The most common site of larval penetration was on the dorsum (*n* = 23 hosts), ranging in location from interscapular to sacral. Limbs (*n* = 4), flanks (*n* = 4), ventrum (*n* = 1), and face (*n* = 1) were less often used as penetration sites. On many occasions, I observed squirrels attempting to evade flies by running rapidly, making quick darting turns, and flipping onto their backs to dislodge landing flies; ultimately, squirrels took refuge underground. Due to the distance from which observations were made, I was unable to identify the species of fly harassing the squirrels.

Penetration mechanism and developmental rate of larval *N. citellivora* are not known. First instars of *Wohlfahrtia* species that parasitize mammals are able to penetrate intact skin on infants but seem to require an entry site, such as a cuterebrid warble, on subadult and older animals (Boonstra, 1977; Shewell, 1987), though Ruiz-Martinez et al. (1989) suggested that mouth hooks may aid penetration. On none of seven Richardson's ground squirrels that had been last captured within 8 days of detecting myiasis had damaged skin been noted in the area subsequently infested. Larvae grew rapidly during their brief period on the host and did not require a still-living host to complete development. The average lengths of larvae were 2.6 ± 0.4 mm for first instars (*n* = 809 from five hosts), 5.1 ± 1.3 mm for second instars (*n* = 644 from 11 hosts), and 10.4 ± 2.0 mm for third instars (*n* = 564 from 11 hosts). Based on observations of larval growth of *N. citellivora* on carcasses, I estimate the interval from larviposition to host death to be ≤7 days. The first instar is brief in most sarcophagids, with larvae molting to the sec-
ond instar within 24 h of larviposition (Ruiz-Martinez et al., 1989), so I assumed that hosts with predominantly first-instar *N. citellivora* had been struck within the previous 1–2 days. On three such squirrels whose carcasses were maintained at ambient temperature, larvae reached the migratory stage in 6 days. The briefest interval between capture of an apparently uninfested squirrel and its discovery in a moribund condition was 6 days. Larvae on moribund squirrels became migratory after 1–3 days, then pupated 3–5 days after migrating off the carcass. Due to the rapidity with which squirrels became moribund and the likelihood that some animals died underground, presumably the prevalence of myiasis exceeded the 8.6% rate noted for juveniles.

Infested Richardson’s ground squirrels seemed unable to prevent the progress of myiasis and apparently did not remove larvae. Although failure to remove larvae could be attributed to the location of many strikes on inaccessible regions of the dorsum, those squirrels with infestations in the limbs showed no evidence of cleaning the wound. Only one squirrel exhibited signs indicative of possible intervention to limit the infestation; the skin on a large (40 by 40 mm) area of the left shoulder was missing and the exposed muscle was covered with coarse particles of shale, suggesting the squirrel had scraped the skin off the shoulder. Third-instar *N. citellivora* were located under the dried edges of the surrounding skin.

Cutaneous myiasis by sarcophagid larvae rarely has been reported for small rodents in North America. However, larvae of *Wohlflahrtia vigil* are known to cause fatal myiasis in adult and subadult *Microtus townsendii* and in nesting *M. pennsylvanicus* (Boonstra, 1977; Craine and Boonstra, 1986). My observations indicate that *Neo-bellieria citellivora* is a lethal parasite of Richardson’s ground squirrels. Age- and sex-specific differences in the active seasons of squirrels resulted in differential vulnerability of adults and juveniles to parasitism such that *N. citellivora* had little impact on mortality of adult squirrels, but it was a major cause of mortality for juveniles, especially males, from late June through September in one population of Richardson’s ground squirrels in southern Alberta.

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