Distribution of the Bot Fly *Cuterebra emasculator* (Diptera: Cuterebridae) in South Carolina[1]

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ABSTRACT Larvae of the bot fly *Cuterebra emasculator* Fitch infest tree squirrels and chipmunks from the Atlantic Ocean to just west of the Mississippi River and from southern Canada to the Gulf Coast of the United States. Whether the species is present in all states and provinces in this region is not well documented. Because there are few published records of *C. emasculator* in South Carolina, we gathered data on its occurrence in each county by obtaining reports of bot fly-infested squirrels from wildlife rehabilitators, veterinarians, wildlife biologists, county extension agents, hunters, and other wildlife-oriented people. The results indicate that *C. emasculator* infests squirrels, especially the eastern gray squirrel (*Sciurus carolinensis* Gmelin), throughout the state. In South Carolina there apparently are no bot fly-free refugia (at the scale of counties) where squirrels might escape from *Cuterebra* parasites.

KEY WORDS bot fly, *Cuterebra emasculator*, Cuterebridae, Diptera, distribution, parasite/host association, rodent, *Sciurus*, squirrel

There is strong ecological interest in determining whether populations of potential host species avoid parasites by colonizing areas lacking these natural enemies (Grenfell & Gulland 1995, Clayton & Moore 1997, Hassell 2000, Poulin et al. 2000). Such "allopatric escape" might occur especially when the interacting organisms show considerable taxonomic divergence, such as mammalian hosts and their arthropod parasites, particularly those that live independent of a host during part of their life cycle (Arlian & Vyszenski-Moher 1987, Marshall 1987). In these cases, interspecific differences in environmental requirements might allow a host species to expand its range beyond the limits of its parasites.

Cuterebra (Diptera: Cuterebridae) bot flies, specialized, obligate parasites of rodents and lagomorphs throughout North America (Catts 1982, Sabrosky 1986), would appear to be good candidates for investigating allopatric escape. Typically, each *Cuterebra* species infests only one or a few host species, and only the larval stage is associated with the host. Thus, to examine congruence in the geographic ranges of an arthropod parasite and its mammal hosts, we focused on one bot fly species, *Cuterebra emasculator* Fitch, which occurs from the Atlantic Ocean to just west of the Mississippi River, and from southern Canada to Florida (Sabrosky

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1986). Although the range of this species has been broadly defined, its actual distribution within this region is not well documented.

Larvae of *C. emasculator* commonly parasitize eastern gray squirrels (*Sciurus carolinensis* Gmelin), fox squirrels (*Sciurus niger* L.), and eastern chipmunks (*Tamias striatus* (L.)), whereas red squirrels (*Tamiasciurus hudsonicus* (Erxleben)) and flying squirrels (*Glaucomys sabrinus* (Shaw) and *G. volans* (L.)) appear to be much less frequently affected (Dorney 1965, Sabrosky 1986, Forrester 1992, Coyner 1994, Slansky & Kenyon 2000, 2002, F. Slansky & L. R. Kenyon, Gainesville, Florida, unpublished data). Although each of these potential hosts (except *G. sabrinus*) occur in South Carolina (Brown 1997, Webster et al. 1985, B. Mowder, Charleston, South Carolina, personal communication), the main reference work on *Cuterebra* in North America (Sabrosky 1986) lists no published or unpublished records of *C. emasculator* for the state. The apparent absence of this bot fly from South Carolina seemed unusual in that *C. emasculator* has been documented from adjacent North Carolina (Allison 1953, Parker & Holliman 1971, Sabrosky 1986) and Georgia (F. Slansky, unpublished data), and from nearby Tennessee (Sabrosky 1986). Indeed, subsequent to reviewing the records for *C. emasculator* in Sabrosky (1986), we located two publications (Webster et al. 1985, Cummings & Yarrow 1998) that mention bot flies as parasites of squirrels in South Carolina, but neither provides distributional data for the species. In addition, the Clemson University Arthropod Collection contains four samples of preserved *Cuterebra* larvae from squirrels, all from Pickens county in the northwest corner of South Carolina (J. C. Morse, Dept. Entomology, Soils and Plant Sciences, Clemson Univ., personal communication). These undoubtedly are *C. emasculator*, as this is the only species of *Cuterebra* typically parasitizing North American tree squirrels (Sabrosky 1986). This limited information indicated that *C. emasculator* is present in South Carolina, but perhaps is restricted to the northwestern part of the state.

If *C. emasculator* had such a limited distribution in South Carolina compared with the broader ranges of its hosts, this finding would provide an example of allopatric escape by populations of host species from one of their specialized natural enemies, and it would raise the question of what factors might be responsible for this pattern. However, before concluding that allopatric escape does occur within the state, we decided that a more thorough assessment of the range of *C. emasculator* in South Carolina was necessary. Thus, we gathered data on its presence on a county-by-county scale by contacting wildlife rehabilitators, veterinarians, wildlife biologists, county extension agents, hunters and other wildlife-oriented people to determine whether they had ever seen bot fly-infested squirrels in South Carolina and in which counties their observations were made.

This approach was possible because, in contrast to many other parasitic arthropod and mammal host associations, the relationship between *C. emasculator* and its hosts offers several features that facilitate verification of the parasite's presence. First, *C. emasculator* is the only bot fly parasitizing tree squirrels and eastern chipmunks, so it is not necessary to remove larvae from a host for species identification. Second, infestation is often readily observable in a free-ranging squirrel, even at a distance of several meters, because bot fly larvae form large lumps (warbles) in a squirrel's hide, frequently in the shoulder or flank (Fig. 1). Their liquid excretion oozes through a warble pore (Fig. 2), which the larvae cut with their pointed mouth hooks. The warbles and the skin around them are often

Fig. 1. Eastern gray squirrel foraging at Hilton Pond Center (York County, South Carolina) with midsized *Cuterebra emasculator* bot fly warbles (open lesions) in neck and shoulder regions. (Photo: B. Hilton Jr.)

hairless, especially if they can be reached and scratched by the host squirrel's hind legs (Fig. 3; Slansky & Kenyon, 2000, 2001a). This visible confirmation of larval infestation is fortuitous, as the adult flies are seldom seen in the wild (Sabrosky 1986, Slansky & Kenyon 2000). There is a viral disease (squirrel fibromatosis or pox) that also causes lesions on squirrels, but these typically differ from warbles in appearance, intensity and location on the host (Slansky & Kenyon 2001b). In addition, squirrel pox is rarely seen in South Carolina (personal communication from several wildlife rehabilitators; see acknowledgments). Thus, it is unlikely that a bot fly-infested squirrel in South Carolina would be misdiagnosed. Third, tree squirrels, especially *S. carolinensis*, are relatively common in urban, suburban and rural areas, and are frequently observed raiding bird feeders or drinking from bird baths. Fourth, injured, ill, and orphaned squirrels are often brought to wildlife rehabilitators or veterinarians for care. Fifth, squirrels are hunted as a small game species, allowing hunters to also examine them firsthand. Taken together, these factors make the association between *C. emas-*

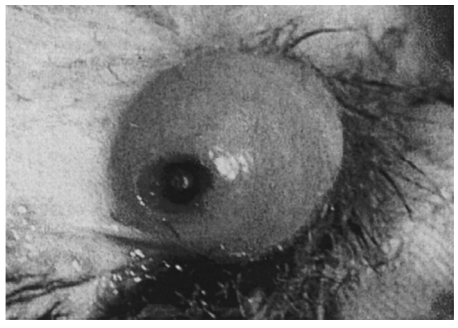

Fig. 2. Warble of *C. emasculator* on an eastern gray squirrel, with the posterior end of the dark brown third instar larva filling the warble pore. The lighter-colored structures in the center of the warble pore are the larva's respiratory spiracles. (Photo: F. Slansky & L. R. Kenyon)

Fig. 3. Eastern gray squirrel (at a seed feeder) heavily infested with larvae of *C. emasculator*. (Photo: F. Slansky & L. R. Kenyon)

culator and its hosts unique in that a large group of people can make reliable observations relevant to determining the presence of this parasite in a given area.

Materials and Methods

We gathered information over a 17-month period (May 2002 to September 2003). To identify potential contacts for this study, we used membership lists of the two major wildlife rehabilitation organizations with members in South Carolina (National Wildlife Rehabilitators Association and the International Wildlife Rehabilitation Council), two wildlife rehabilitator web site lists ("How To Locate a Wildlife Rehabilitator" at http://www.tc.umn.edu/~devo0028/contact.htm and "Wildlife Rehabilitation Centers in the U.S." at http://www.southeasternoutdoors.com/rehab_usa.html), other web sources, and networking. We contacted most people via e-mail, but telephoning was used when e-mail addresses were unavailable.

For e-mail inquiries, we provided a brief description of bot fly infestation of squirrels and links to web sites having additional information about this phenomenon (Slansky & Kenyon 2001a,b). For telephone contacts, symptoms of bot fly infestation of squirrels were described prior to gathering information if the person was unfamiliar with this condition. Many contacts were asked only about sightings of "bot fly-infested squirrels" regardless of species. However, because of their often-extensive experience with these animals, wildlife rehabilitators and wildlife biologists were asked to provide information on the different species of squirrels (*S. carolinensis*, *S. niger*, and *G. volans*) and chipmunks (*T. striatus*). Information about red squirrels (*T. hudsonicus*) was not specifically requested because they occur primarily in the northwest corner of the state (Brown 1997, Webster et al. 1985) and thus are not commonly observed or treated by wildlife rehabilitators (B. Mowder, personal communication); in addition, they are seldom infested by *Cuterebra* (Dorney 1965, B. Mowder, personal communication). Records were not included in the data analyses if a person indicated he or she seldom observed squirrels. Differences among the frequencies of infestation reports for the host species were tested for statistical significance using the chi-square test (Zar 1984).

Results

Of the 104 reports we received, 97 were positive for sightings of bot fly-infested squirrels, with at least one positive report coming from each of South Carolina's 46 counties. The number of infestation reports for each county is given here in parentheses: Abbeville (1), Aiken (1), Allendale (1), Anderson (3), Bamberg (2), Barnwell (1), Berkeley (1), Beaufort (4), Calhoun (2), Charleston (5), Cherokee (2), Chester (2), Chesterfield (1), Clarendon (2), Colleton (3), Darlington (3), Dillon (1), Dorchester (2), Edgefield (1), Fairfield (1), Florence (2), Georgetown (4), Greenville (5), Greenwood (2), Hampton (3), Horry (4), Jasper (3), Kershaw (2), Lancaster (2), Laurens (1), Lee (1), Lexington (3), Marion (1), Marlboro (2), McCormick (2), Newberry (1), Oconee (2), Orangeburg (3), Pickens (2), Richland (2), Saluda (1), Spartanburg (3), Sumter (3), Union (1), Williamsburg (2), and York (3).

Of respondents who categorized the species of squirrels they had observed, 100% (21 of 21) had seen eastern gray squirrels, 65% (13 of 20) fox squirrels, 91% (19 of 21) flying squirrels, and 38% (6 of 16) eastern chipmunks. Of these records, the percentage (and number) indicating that they had seen bot fly-infested animals of each species was: 86% (18 of 21) eastern gray squirrels; 23% (3 of 13) fox squirrels; 11% (2 of 19) flying squirrels; and 0% (0 of 6) eastern chipmunks. Based on these data, infested eastern gray squirrels are much more likely to be observed than fox squirrels ($\chi^2 = 37.8$; $P < 0.001$), flying squirrels ($\chi^2 = 7.8$; $P < 0.01$) or chipmunks (no infestation reports).

Discussion

These results clearly demonstrate the widespread occurrence of *C. emasculator* throughout South Carolina. The data we gathered concur with two publications that mention bot flies as parasites of squirrels in the state without providing distributional information (Webster et al. 1985, Cummings & Yarrow 1998), and with unpublished records of this species' presence in Pickens County, as indicated by four samples of larvae in Clemson University's Arthropod Collection. The results of our study extend the range of *C. emasculator* to the 45 other counties of the state.

Reports we received of bot fly-infested squirrels appeared very reliable because most came from wildlife rehabilitators, wildlife biologists, county extension agents, and others having direct experience with squirrels parasitized by these insects. In contrast to the definitive nature of the data documenting the presence of squirrels parasitized by *C. emasculator*, the few "no infestation observed" reports we received from squirrel observers demonstrate only that they had not seen bot fly-infested squirrels and do not prove that these parasites are absent from an area.

Although our study focused on determining the distribution of *C. emasculator* in South Carolina, limited data were collected on the frequency of infestation reports for the various squirrel species. It is important to note that our sample sizes are relatively small ($\leq$21) and the differences may reflect sampling bias, even though they are expressed on a relative basis. Nonetheless, the species ranking found here (gray squirrels > fox squirrels > flying squirrels) reflects what appears to be a similar trend in Florida (F. Slansky & L. R. Kenyon, unpublished

data) and may indeed indicate a biological difference in susceptibility to infestation among these squirrel species.

Habitat preferences can influence the probability of a host being encountered by parasites and other natural enemies. The habitat of fox squirrels typically differs from that of eastern gray squirrels (although there can be some overlap; Woods 1980, Flyger & Gates 1982, Webster et al. 1985) and this could affect the incidence of parasitism of these two species if *C. emasculator* prefers to oviposit in gray squirrel habitat. Flying squirrels may occur in the same habitats as the two *Sciurus* species (Woods 1980) but appear to have a very low incidence of bot fly parasitism (present study; Forrester 1992, Slansky & Kenyon 2000, F. Slansky & L. R. Kenyon, unpublished data; B. Mowder, personal communication). Animals are exposed to *Cuterebra* by contacting eggs laid on habitat substrates. Their body heat can cause the eggs to hatch rapidly and the larvae may then infest the animal (Catts 1982). Perhaps the nocturnal activity of flying squirrels (both gray and fox squirrels are diurnal) reduces their susceptibility to becoming parasitized. For example, *C. emasculator* eggs may hatch less readily in darkness than in light, but this hypothesis remains to be investigated. Whether the species of tree squirrels differ in their physiological resistance to *C. emasculator* parasitism apparently has not been tested experimentally, but it is known that certain rodent species are refractory to artificial infestation by larvae of *Cuterebra* species not normally parasitizing them (Capelle 1970, Baird 1972, Gingrich & Barrett 1976). Clearly, additional research is needed to quantify infestation frequencies of these tree squirrel species in the field and to identify the mechanisms responsible for any differences that are found.

Given the statewide distribution of *C. emasculator* in South Carolina, there would appear to be no bot fly-free refugia for squirrels in the state at the county scale. In contrast, in Florida *C. emasculator* appears to be absent from or extremely rare in most southern counties despite the presence of potential tree squirrel hosts (F. Slansky & L. R. Kenyon, unpublished data). Reasons for this truncated distribution of *C. emasculator* in Florida are unknown. A few *Cuterebra* species that infest other mammals range into extreme south Florida (Sabrosky 1986), indicating there is no insurmountable geographic or biological barrier preventing *Cuterebra* bot flies from occurring in this area if their hosts are present. The implications for the population biology of squirrels avoiding these parasites also are unknown. *Cuterebra* larvae can affect the host animal by causing anemia and altering movement and other behaviors, including possibly interfering with reproduction, but these effects are most likely to have biological significance only in the few host individuals that become heavily infested (F. Slansky & L. R. Kenyon, unpublished literature review).

Despite the apparent total range overlap between *C. emasculator* and their typical host species in South Carolina, it is possible that squirrels and chipmunks could escape from or at least incur reduced parasitism by colonizing particular habitats less used by bot flies. In Mississippi, for example, eastern gray squirrels had a higher incidence of parasitism by *C. emasculator* in hardwood than in pine-hardwood or pine habitat of bottomland or flatland topography (Jacobson et al. 1981). Individuals of two species of ground-dwelling small mammals (the deer mouse, *Peromyscus maniculatus* (Wagner), and the southern red-backed vole, *Clethrionomys gapperi* (Vigors)) inhabiting upland hardwood (maple, beech, and birch) habitat avoided *Cuterebra* parasitism, in contrast to those in neighboring

lowland softwood sites dominated by spruce and fir (Bowman 2000; for other examples of 'habitat escape' from *Cuterebra* see Clark & Kaufman 1990 and Wolf & Batzli 2001). Whether squirrels and chipmunks in South Carolina also experience such habitat escape apparently has not been investigated (we did not address this issue in the present study) but these host species do experience seasonal escape from *C. emasculator*. This parasite is apparently univoltine throughout its range, with larvae infesting host animals only from July or August through October or November; the remaining months are spent in pupal diapause in the soil (Bennett 1955, 1972, Sabrosky 1986).

The association between *C. emasculator* and the animals it infests has distinct features that appear to make it an ideal system in which to study congruence between the geographic ranges of a specialized arthropod parasite and its mammalian hosts. Although South Carolina can now be added to the list of states in which *C. emasculator* is prevalent, the distribution of *C. emasculator* in eastern North America remains incompletely known (Sabrosky 1986). Additional research is necessary to more thoroughly document this species' presence in other states and counties, and within the Canadian provinces. More information is also needed on local habitat preferences and seasonal occurrence of *C. emasculator* throughout its range. Longer-term changes in its abundance, seasonality, and distribution, and possible associations with global warming, are also of interest.

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