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Seasonality of *Ormia depleta* and Limits to Its Spread

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Ormia depleta **(Wiedemann) (Diptera: Tachinidae), a South American fly that homes on the calling songs of its hosts, was brought from Piracicaba, Brazil; colonized; and released in Florida for the biological control of *Scapteriscus* spp. mole crickets. It became established at some release sites and rapidly spread through most of peninsular Florida. The seasonal distributions of phonotactic females in Florida differed from the single summer peak recorded at Rio Claro and Piracicaba, Brazil (23° S). Near Bradenton (27° N), spring and fall peaks with a summer hiatus were quickly established and remain evident. At two sites near Gainesville (30° N), a strong fall peak and a modest-to-none spring peak developed. Peaks of phonotactic females seem to follow times of peak host availability and sometimes coincide with minima of host availability. Limits to geographical expansion of *O. depleta* are poorly understood. At Gainesville, the site of earliest introduction, establishment was rapid and sound-trap catches increased for the first 3 years, exceeding 1000 per year at one site. Catches then declined for 3 years, almost reaching zero in 1994. On the other hand, annual sound-trap catches of *O. depleta* at Bradenton exceeded 1000 in <2 years and have remained above that level for 5 years. Winters in Gainesville are more severe than those in Bradenton, but minimum winter temperatures in Gainesville were substantially lower during *O. depleta*'s increase than during its decline. Perhaps mild winters cause the flies to become active early—only to starve for lack of adequate winter nectar sources. *O. depleta* may yet spread to the northern limits of its *Scapteriscus* hosts as present populations adapt to new environments. Or farther spread may require that new strains be introduced from more southerly sites in South America.** © 1996 Academic Press, Inc.

KEY WORDS: ***Ormia depleta; Scapteriscus vicinus; Scapteriscus borellii; Scapteriscus imitatus;*** **biological control; seasonality; geographical variation; geographical limits.**

INTRODUCTION

Ormia depleta (Wiedemann) is a South American tachinid that attacks mole crickets of the genus *Scapteriscus* (Fowler, 1987a). Females locate hosts by their calling songs and deposit larvae on or near the host. After it was identified as a likely biocontrol agent for *Scapteriscus vicinus* Scudder and *Scapteriscus borellii* Giglio-Tos in the southeastern United States, *O. depleta* was imported from Piracicaba, Brazil, released at numerous sites in Florida, became established at some, and soon spread throughout south and central peninsular Florida (Frank *et al.,* 1996).

The climate of Piracicaba is similar to that of central Florida, though of course the seasons are 6 months out of phase. The seasonal occurrence of adults of host species is likewise similar (Fowler, 1987b). The southward distribution of *O. depleta* in South America is poorly known. The only records significantly south of Piracicaba are from San Lorenzo, Paraguay (25° S) (Fowler and Kochalka, 1985). Negative data usually mean little for *Ormia* spp. because they are seldom collected by ordinary means. However, A. Silveira-Guido, who was paid by the University of Florida to survey Uruguay (31–35° S) for mole crickets and their natural enemies, screened >1600 *S. vicinus* and *S. borellii* for parasitoids and found no parasitism by *Ormia* (personal communications, 1984, 1985).

This paper deals with the seasonal occurrence of larvipositing females of *O. depleta* in Brazil and Florida and with population trends and limits to northward spread in Florida.

MATERIALS AND METHODS

Seasonal Distribution of Larvipositing Females

By far the most efficient way to monitor larvipositing *O. depleta* females is to trap them as they come to synthesized, amplified songs of *S. vicinus* or *S. borellii* (Frank *et al.,* 1996). The synthesizers/emitters used in this study were compact (15 × 13 × 10 cm) and could be operated with battery or mains current (Walker,

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1982). One way to catch *O. depleta* attracted to an emitter is to put the emitter in a plastic bag smeared with a sticky material, such as Tack Trap (Animal Repellents, Griffin, GA). However, removing and identifying the ensnared flies is time consuming and messy, and the flies must be sacrificed. Therefore, most of our trapping was with live traps that gave attracted flies the opportunity to pass through two valves into a removable container (Walker, 1989).

At Piracicaba, Brazil (22° 43′ S latitude) from August 1988 to April 1989, two *S. vicinus* and two *S. borellii* emitters were operated 2 to 6 times each month (usually 3) with one of each type provided with a live trap and the other with a sticky bag. Traps were operated for 90 min on each night of trapping, beginning 15 min before dark. Monthly totals of trap nights and numbers of flies caught were used to estimate the number of flies that would have been caught had a single average trap been operated every night: (no. flies/no. trap nights) × no. days in the month.

At Gainesville, Florida (29° 40′ N latitude), *O. depleta* was monitored at two long-established mole cricket trapping stations, GVA and GVC (Walker *et al.,* 1983). At each station live traps were installed over the emitters (one *S. vicinus* and one *S. borellii*), which were operated nightly by timers. At GVA, the traps were set in place May 5, 1988, a few days after the first release of *O. depleta,* and the emitters were operated from sunset until sunrise. At GVC, 3.9 km WNW of GVA, live traps were installed February 12, 1989, and the emitters operated for 2 h beginning at sunset.

The third long-established mole cricket trapping station was at Bradenton, Florida (BDN) (27° 27′ N latitude). Here *O. depleta* monitoring began October 28, 1988, was inadvertently discontinued during much of 1989, and was resumed in January 1990. Emitters were operated for 2 h beginning at sunset until June 25, 1990, when they were put on a sunset-to-sunrise schedule.

In all cases, except BDN prior to June 25, 1990, captured flies were removed from the trapping site to prevent recaptures.

Population Trends of O. depleta and Northward Limits

The Gainesville sound trapping stations are apparently near the northern limits for the *O. depleta* biotype introduced from Piracicaba. To ascertain what conditions permit or foreclose survival from one year to the next, we compared the annual changes in numbers of *O. depleta* trapped at these stations to changes in winter weather. In addition, trap-line studies by Frank *et al.* (1996) augmented the trapping station data on continued survival or extinction of *O. depleta* populations.

Population Trends of Hosts

The standardized sound trapping stations used to monitor the seasonal distribution and population trends of *O. depleta* were originally established to monitor mole crickets (Walker, 1982; Walker *et al.,* 1983). The stations continued that function in this study as counts of trapped *S. vicinus* and *S. borellii* were used to estimate their population trends.

RESULTS AND DISCUSSION

Figure 1A shows the monthly distribution of *O. depleta* at Piracicaba. Figures 2–4 show it at Gainesville and Bradenton. Figures 2F, 3F, and 4E show the average distribution for the four most bountiful years at each of the Florida sites. Figure 5 displays annual numbers (March to February) of *O. depleta* captured at the three Florida trapping stations. Figure 6 displays numbers of *S. vicinus* and *S. borellii* captured at the same stations from August 1979 to July 1994.

In November 1991, trap lines were run outward from GVA in four directions and caught *O. depleta* as far as 27 km to the north, 16 km east, 14 km south, and 38 km west. On June 22 and July 3, 1992, trap lines from Gainesville 80 km south to Red Level and from Gainesville 69 km south to near Belleview caught no flies (Frank *et al.,* 1996).

Seasonal Distribution of Larvipositing Females

Traps were not run in May, June, and July (=autumn) at Piracicaba, but catches of phonotactic females

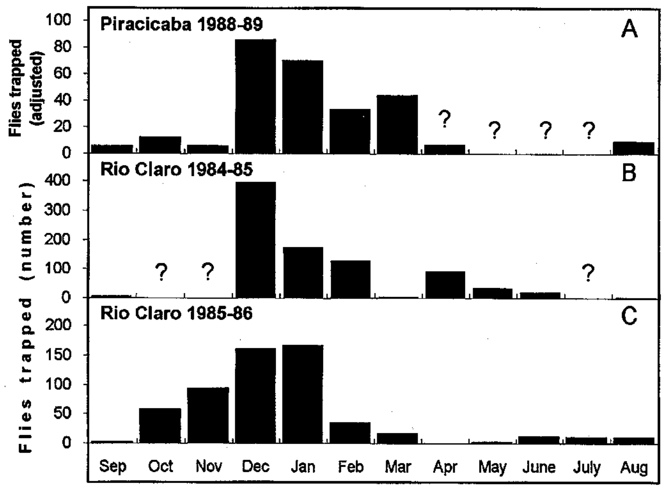

FIG. 1. Seasonal distribution of phonotactic *O. depleta* females in southern Brazil. Months have been rotated 180° from those in Figs. 2–4 to put months of similar season in corresponding positions. (A) Piracicaba, 1988–1989. No data were taken in May, June, or July. The April data were from a single night's trapping early in the month and were not extrapolated to estimate the catch for the month. (B) Rio Claro, 1984–1985 (Fowler, 1988). (C) Rio Claro, 1985–1986 (Fowler, 1987).

of *O. depleta* from the remaining months suggest a single, summertime peak—viz., December to March, corresponding to June to September in the Northern Hemisphere (Fig. 1A). Earlier data, from nearby Rio Claro, showed a similar single peak (Figs. 1B and 1C) (Fowler, 1987a, 1988).

At none of the Florida sites (Figs. 2–4) did the seasonal distribution of phonotactic *O. depleta* assume the single summer peak evident in Brazil. A late fall, early winter (October–January) peak developed at all three sites, and a late spring (May–June) peak was strongly evident at BDN (Fig. 4) and weakly to scarcely evident at GVA and GVC (Figs. 2 and 3). Because the fall/winter peak bridged the end of a calendar year, we based our analyses of annual changes in seasonality on "*depleta* years," i.e., years that start in March of one year and end in February of the next.

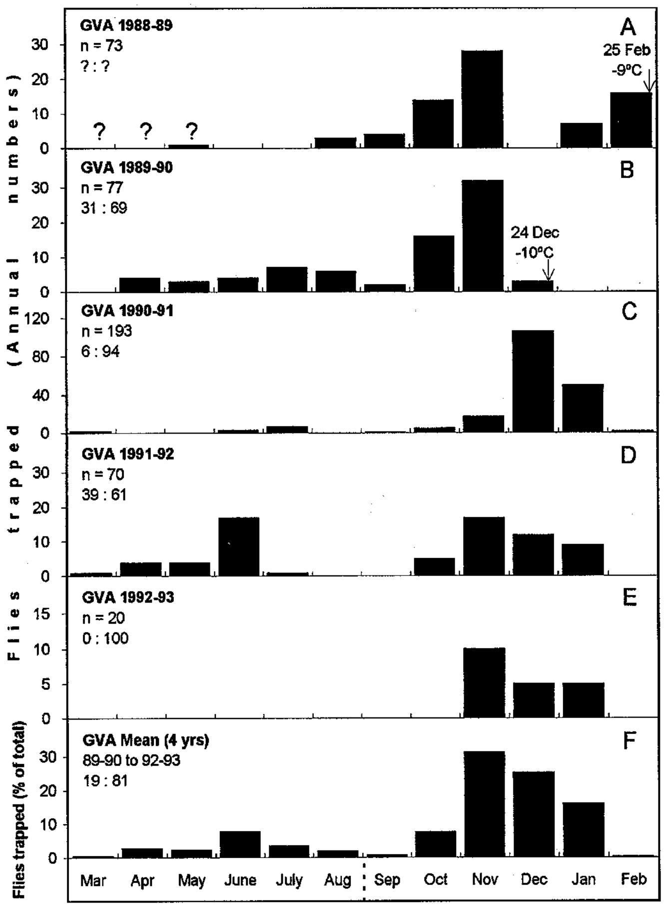

FIG. 2. Seasonal distribution of phonotactic *O. depleta* females at station GVA, Gainesville, Florida. The month at extreme left is March, the beginning of the "*depleta* year" (see text). In the upper left of each graph are the percentages of the year's catch caught in March–August and in September–February. (A–E) 1988–1989 to 1992–1993. The total catch for each year (*n*) is given at upper left. In A, the question marks indicate no data or a fly that may have been one of those originally released. (F) Mean monthly distribution (expressed as percentage of total) for 1989–1990 to 1992–1993.

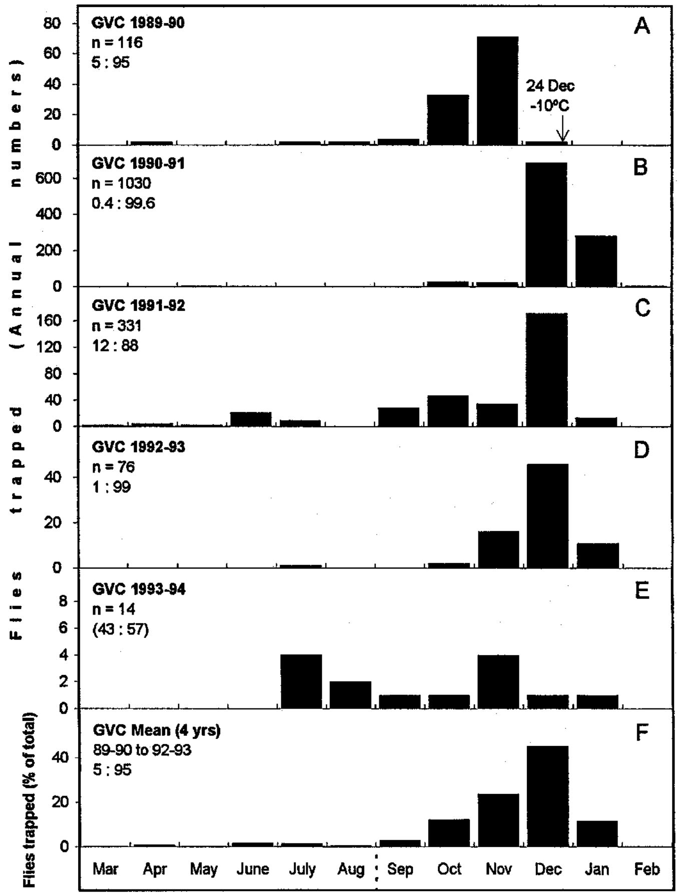

FIG. 3. Seasonal distribution of phonotactic *O. depleta* females at station GVC, Gainesville, Florida (conventions as in Fig. 2). (A–E) 1989–1990 to 1993–1994. (F) Mean monthly distribution for 1989–1990 to 1992–1993.

At Bradenton, spring and fall peaks were evident from the start, but the percentage of the total catch caught in the first 6 months of the *depleta* year increased from 35% in 1990–1991 to 75% in 1993–1994 (Figs. 4A–4D). During the 4 years of monitoring at BDN temperatures apparently never fell so low as to eliminate phonotactic females. On December 25 and 26, 1989, the temperature dipped to −4°C, but captures in March and April 1990 were similar to those for the same months following milder winters (Figs. 4A–4D).

At Gainesville, on the other hand, record lows, of −9 and −10°C, occurred on February 25, 1989 and December 24, 1989 (Figs. 2A, 2B, and 3A), and in each case no more flies were captured for the next >2 mo.

Except for occasional winter kill by record low temperatures, the causes of increases and decreases in phonotactic females of *O. depleta* are far from clear, but differences in seasonalities among the sites that were studied could give clues to causes. In particular, the differences might reflect different seasonal distributions of host mole crickets. Seasonality of mole crickets can be deduced from the numbers flying to sound traps

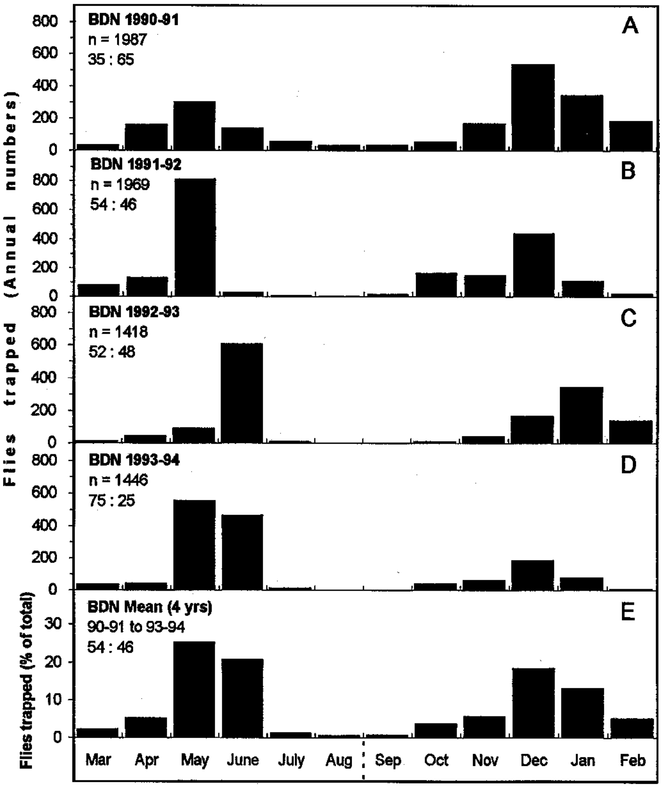

FIG. 4. Seasonal distribution of phonotactic *O. depleta* females at station BDN, Bradenton, Florida (conventions as in Fig. 2). (A–D) 1990–1991 to 1993–1994. 1989–1990, the first year of establishment, is omitted because no data were collected during August–December. (E) Mean monthly distribution for 1990–1991 to 1993–1994.

(Walker *et al.,* 1983). Maxima of flying and calling generally coincide in *Scapteriscus* spp., probably because calls function primarily in attracting *flying* females. In keeping with this, males of *S. vicinus* and *S. borellii* direct their calls upward using special acoustical burrows (Forrest, 1991), and *Scapteriscus abbreviatus,* the only flightless species studied, makes no calling song.

Seasonality in Brazil. Of the three *Scapteriscus* spp. that occur at Piracicaba and Rio Claro, *S. vicinus* and *S. borellii* do most of their flying in spring, whereas *S. imitatus* Nickle & Castner flies mostly in winter (Fowler, 1987b). If flying by *Scapteriscus* spp. in southern Brazil accurately estimates calling, *O. depleta* becomes most abundant there at a time when calling hosts are practically absent. This could be viewed simply as a parasitoid peak lagging a host peak (Nicholson and Bailey, 1935). However, the host peak and following trough are not dependent on the parasitoid. The hosts are univoltine and apparently have a single, though prolonged, period of mating activity each year (Fowler, 1987b; Walker *et al.,* 1983). In other words, times of host abundance are predictable, yet *O. depleta* has not incorporated that information into its suite of adaptations. It is noteworthy that the abundance of Brazilian *O. depleta* larvipositing females at times of host scarcity is matched by three *Ormia* spp. native to northern Florida—namely, *Ormia ochracea* (Bigot) on *Gryllus rubens* Scudder, *Ormia dominicana* Townsend on *Orocharis luteolira* Walker, and *Ormia lineifrons* Sabrosky on *Neoconocephalus triops* (L.) (T. J. Walker, unpublished).

Seasonality at Bradenton. Here each generation of *S. vicinus* and *S. borellii* begins flying in September to November but flies mostly in early spring. Adults, and calling and flying, are nearly absent in June, July, and August. In their analyses of 2 years of data, Walker *et al.* (1983) reported fall peaks that were 12 and 32% of the spring peaks in *S. borellii* and 1 and 3% in *S. vicinus.* The seasonal distribution of *O. depleta* (Fig. 4) lags the peaks of its hosts by about a month in the spring and a month or more in the fall. As in Brazil, though less pronounced, fly abundance fails to track host availability.

Seasonality at Gainesville. The seasonality of mole cricket flights in Gainesville is much the same as that in Bradenton except that *S. borellii* starts and stops its spring flights a bit later (Walker *et al.,* 1983). Yet *O.*

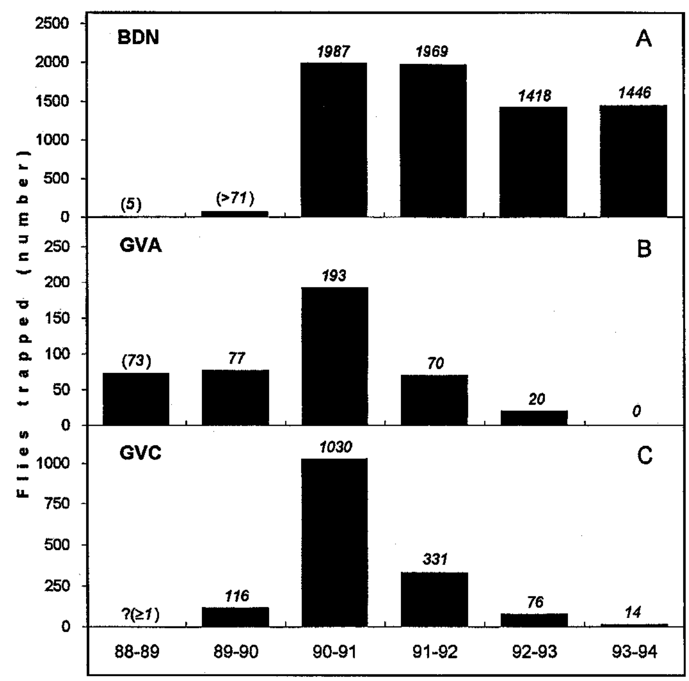

FIG. 5. Changes in numbers of *O. depleta* trapped annually (March to February) at Bradenton and Gainesville, Florida, 1988–1989 to 1993–1994. Numbers that are in parentheses are for incomplete trapping data. The question mark indicates that the trapped fly may have been one of those released. (A) BDN. The earliest proof of establishment was in February 1989. Traps not operated August to December 1989; though flies were caught in April, June, and July 1989. (B) GVA. First proof of establishment was August 1988. (C) GVC. Traps not operated during 1988.

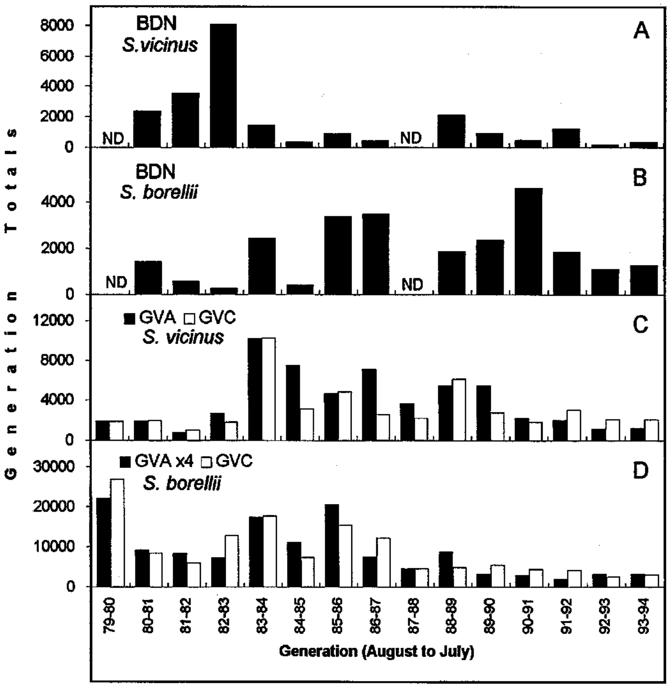

FIG. 6. Changes in numbers of host mole crickets trapped per August-to-July generation at Bradenton (A, B) and Gainesville (C, D), Florida, 1979–1980 to 1993–1994. ND, no data for that generation. Numbers of *S. borellii* captured at Gainesville site GVA were multiplied by 4 to give their trends the same visibility as those at GVC.

depleta usually lacked the spring peak that always amounted to 35% or more of the annual total at Bradenton. A spring peak of this prominence occurred at GVA only in 1991–1992. At GVC, the spring peak never exceeded 12% in a year when 50 or more *O. depleta* were captured. Possible explanations include winter cold or food shortages killing most *O. depleta* or Gainesville's climate inducing prolonged diapause.

Population Trends and Northward Limits

At Bradenton (Fig. 5A), *O. depleta* became well established during 1989–1990, but during much of 1989 the BDN fly traps were not operated. Thus, the BDN records of abundance begin in 1990–1991, when nearly 2000 flies were captured. The next *depleta* year yielded a similar number of flies, and the following 2 years yielded about 1400 each. Once established, the *O. depleta* population remained strong. The somewhat lower numbers the last 2 years coincide with lower numbers of *S. vicinus* and *S. borellii* trapped at the same station (Figs. 6A and 6B).

At the Gainesville stations, populations peaked in 1990–1991 and then declined (Figs. 5B and 5C), nearly to extinction. Trap lines in fall of 1991 caught flies 14–38 km from GVA in each of four directions, but two lines of 11 traps, from Gainesville south in June and early July 1992, yielded nothing (Frank *et al.,* 1996). The most recently collected *O. depleta* at either station was January 11, 1994, at GVC until captures resumed in mid November 1994 at both GVA and GVC. Although the pattern of population increase and decline was similar at GVA and GVC, populations at GVC were approximately fivefold those at GVA. This correlates with GVC lying within extensive habitat suitable for *Scapteriscus* spp., while GVA is an island of suitable habitat within an extensive wooded area.

The decline to near extinction of *O. depleta* at Gainesville cannot be attributed to minimum winter temperatures. The minimum temperatures during the winters of 1988–1989 and 1989–1990 were among the coldest on record (Figs. 2A and 2B), yet in each case the next year's catch was greater. Minimum temperatures for subsequent winters (1990–1991 to 1993–1994) were −5, −7, −4, and −6°C. During the duration of this study the minimum winter temperature at Bradenton was −4°C (December 25 and 26, 1989); the lowest subsequent temperature was −1°C on January 17, 1992. At Rio Claro, the record minimum temperature is −2°C (number of years not known) (Walter and Lieth, 1960).

What then could be responsible for the near demise of *O. depleta* at Gainesville? One possibility is that host populations have been reduced to a level that can barely support an *O. depleta* population. The number of potential hosts has declined substantially (Figs. 6C and 6D), but not nearly to the levels that still support very large populations of *O. depleta* at Bradenton (Figs. 6A and 6B) and substantial populations in southern Brazil (J. H. Frank, observation). A second possibility is that one or more organisms or microorganisms that attack *O. depleta* have increased and nearly eliminated the species from the Gainesville area. However, we have no candidate enemies of this severity nor would we expect such enemies to limit their Florida activities to the latitude of Gainesville. For now our favorite scenario is that when *O. depleta* fails to maintain dormancy in Gainesville winters it starves. Winter nectar sources are fewer in Gainesville than in Bradenton. S. A. Wineriter (pers. comm.) discovered that supplying adult *O. depleta* with artificial nectar (e.g., commercial hummingbird food) greatly prolonged their longevity in laboratory colony cages or in small sealed vials. The success of *O. depleta* following severe winters and its decline after mild winters suggests that cold winters prolong dormancy whereas mild winters allow it to end before essential foods become available. To test this scenario, we need to identify the nectar sources used by *O. depleta* and see if we can enhance spring populations at selected sites in north Florida by providing nectar during winter.

Whatever the cause, the northern boundary of significant populations of *O. depleta* may at times be south of

Gainesville. Perhaps this situation is only temporary, and Florida *O. depleta* will evolve adaptations permitting it to spread to the northern limits of *Scapteriscus* spp. Or perhaps *O. depleta* biotypes at the southern extremes of its South American range already have the necessary adaptations and can be introduced. Indeed, we are now trying to acquire biotypes from as far south as possible in South America.

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