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SEASONAL DEVELOPMENT OF *GRYLLOTALPA AFRICANA* (ORTHOPTERA: GRYLLOTALPIDAE) ON TURFGRASS IN SOUTH AFRICA

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Abstract

The population dynamics (in terms of seasonal development) of *Gryllotalpa africana* Palisot de Beauvois was documented for the first time in South Africa. An irritant drench (soapy water solution) was used to quantify life stage occurrence on turfgrass over a one-year period. Oviposition took place from early October (spring), with eggs incubating for approximately three weeks. Nymphs reached the adult stage from March (late summer) and most individuals overwintered in this stage. Adult numbers peaked in early September (early spring), declining through spring. *G. africana* was therefore univoltine in the study area. The adult population was female biased in spring. The smallest nymphs and adults (in relation to mean length) were collected in December (early summer), while the smallest nymphs (in relation to mean length) occurred in November (late spring).

Key Words: Univoltine, spring oviposition, life stage, turfgrass, mole cricket

Resumen

La dinámica de la población (en terminos del desarrollo estacional) de *Gryllotalpa africana* Palisot de Beauvois fué documentada por la primera vez en Africa del Sur. Una mojada irritante (una solución de aqua con jabón) fué utilizada para cuantificar la ocurrencia de los estadíos de vida en el césped durante un período de un año. La oviposición occurió desde el principio de octubre (la primavera), incubando los huevos por aproximadamente tres semanas. Las ninfas llegaron la étapa adulta desde marzo (al final del verano) y la mayoría de los individuos pasaron el invierno en este estadío. El número más alto de adultos se obtuvo en el principio de septembre (al principio de la primavera), y declinó atravéz de la primavera. Desde entonces, el *G. africana* fue univoltino en la área del estudio. Habian una inclinación viciada hacia las hembras en la primavera. Las ninfas y los adultos más pequeños (en relación al promedio de la longitud) fueron recolectados en diciembre (al principio de verano), mientras que las ninfas más pequeñas (en relación del promedio de la longitud) fueron recolectados en noviembre (al final de la primavera).

Gryllotalpa africana Palisot de Beauvois (African mole cricket) occurs only in Africa (Townsend 1983). The only account concerning the life cycle of this species is from Zimbabwe (Sithole 1986). Some notes on the species in South Africa were provided by Schoeman (1996) and Brandenburg et al. (2002).

Females lay 30-50 oval, white eggs in hardened chambers in the soil (Sithole 1986). Incubation period is temperature dependent, varying from 15-40 days. Nymphs feed on earthworms and roots of plants and under favorable conditions, develop through six instars with wing bud development visible in later instars (Sithole 1986). The nymphal period lasts three to four months. One generation per year is known (Sithole 1986). According to Schoeman (1996), there are approximately 10 instars of *G. africana* in South Africa and research by Brandenburg et al. (2002) showed that burrows of the African mole cricket are typically Y-shaped and range from 100 mm to 230 mm in length. The life and seasonal cycle of *G. africana* has not been investigated in South Africa and no reports on the seasonal development of *G. africana* on African turfgrass are available.

Life cycle, seasonal development and behavior documentations under the name *G. africana* include reports by the United States Department of Agriculture (1974) (U.S.A. potential introduction from Asia), Kim (1993, 1995) (Asia), Muralirangan (1979) (Asia), Tindale (1928) (Australia) and Goodyer (1985) (Australia). It is unknown if these studies refer to "true" *G. africana* from Africa.

Life cycle and seasonal development reports (including voltinism) for similar mole cricket species may vary significantly between geographical areas (Hudson 1987). In a specific area, different species and even different genera may show general life cycle similarity (including voltinism) (Frank et al. 1998). Therefore analysis of variations in life cycle, seasonality, and other factors for species occurring in climates similar to an area of interest may be more useful in estimating these parameters for a population than multiple studies of that species under a range of environmental conditions.

Materials and Methods

Infested kikuyu grass (*Penisetum clandestinum* Hochst ex Chiou) areas at Pretoria Country Club (25°47'16"S; 28°15'28"E) were flushed with soapy water (50 ml Sunlight® (Lever Ponds Pty Ltd., Durban) dishwashing soap/5 liters H_2O/m^2); this is a simple, inexpensive but effective surveillance technique (Short & Koehler 1979). Flushes started at noon with varying numbers of samples per sampling date (number necessary to collect ca. 100 crickets) with equal sampling intensity (10 liters soapy water) at each site over an annual period (Oct 2001-Nov 2002). Sampling was conducted every two weeks. Flushed areas were chosen at random within each site with the exception that no area was sampled twice over the duration of the experiment. Emerging crickets were captured, counted and total length measured from the posterior of the abdomen (excluding cerci) to the distal end of the labrum. Pronotal and abdominal lengths were also measured and recorded. Adults were sexed and females dissected to determine egg and oocyte presence for each sampling date. Oocytes were deemed mature (eggs) when covered by an egg shell (vitelline membrane and chorion). The long axis of mature eggs was generally longer than 2.5 mm. All sampled areas were under similar irrigation programs and soap flushing efficiency was assumed to be homogenous for adults and nymphs between and within sites throughout the study period. Immigration and emigration (especially through flight) were also assumed to be at equilibrium and not to affect absolute cricket sizes and life stage percentages during the study.

Deviation from an equal sex ratio was investigated by the two-tailed binomial distribution [Sokal & Rohlf 1997; "Statistica" Version: 5 (Statsoft, Inc. 1995)]. The Bonferroni method was used to lower the type one error probability for each comparison, resulting in an overall significance level not exceeding 0.05 in the entire series of tests (Sokal & Rohlf 1997).

Results

The life cycle of *G. africana* for each ontogenic stage as a percentage of the total population over an annual period is graphically presented in Fig. 1. Percentages were calculated by using adult and nymphal counts for a specific sampling date. Eggs were not sampled in the field therefore an 'estimate' of egg percentage on that date was calculated as equal to the mean first instar population percentage three weeks (mean egg hatch time) after that date. The egg percentage over time therefore only refers to fertilized eggs and may be subject to considerable variation, as incubation period is temperature dependant (Frank et al. 1998; Potter 1998). Life stage percentages were subsequently determined from the ontogenic ratio obtained. To obtain an annual presentation (from Nov 2001 to Oct 2002), data were therefore needed from Oct 2001 to Nov 2002. Fig. 1 shows 61% adults and 39% nymphs comprised the overwintering population (Jun-Aug). Patchy, relatively small samples (<40 individuals) were obtained during winter, which may contribute to the inconsistent results obtained during that period (Fig. 1). After overwintering, adult numbers (as a population percentage) peaked at 64% and diminished to 1% during Sep/Oct (spring) and Nov/Dec (spring/summer), respectively (Fig. 1). The egg population peaked at the end of Oct (spring) at 41.52%, further following the adult percentage inclination, but with some eggs laid until late Feb (Fig. 1). Oviposited eggs ranged from 2.5-3.5 mm in length. The graph of nymphal percentages showed an approximate direct inverse relationship with the adult-percentage-graph when no eggs were present (Fig. 1). High egg percentages were associated with the lowest nymphal percentages (Fig. 1). *G. africana* had a univoltine life cycle in the study area (Fig. 1). There is a lack of complete percentage overlap for each ontogenic stage at the beginning and end of the period (Fig. 1).

Mean monthly nymph and overall (adult and nymph) total length of *G. africana* for 12 months are shown in Fig. 2. First instars were 5.95 ± 0.218 mm (mean ± SD) long, with a midline pronotal length of 1.52 ± 0.054 mm (data not shown). The mean monthly nymphal length varied from 6.6 ± 2.56 mm to 25.8 ± 3.70 mm from Nov 2001 (first and second instars present) to Oct 2002 (late instars present), respectively (Fig. 2). Nymphs overwintered from early Jun 2002 when they were 23.0 ± 4.16 mm in length (data not shown), averaging 22.1 ± 3.9 mm over the month (Fig. 2). The mean monthly overall (adult and nymph) length was at a minimum (10.3 ± 6.51 mm) and maximum (31.1 ± 5.53 mm) in Dec 2001 and Oct 2002, respectively (Fig. 2). The mean monthly length of sampled nymphs and the total (nymphs and adults) population showed a relative decline during the winter (Fig. 2)). No females were sampled in Jan and Feb 2002, when one male in each month was flushed (resulting in no standard deviation values). Adult males and females were not distinctly segregated by mean length over monthly intervals, except for spring and early summer months, when females tended to be longer (data not shown). Males and females measured (mean ± SD) 35.91 ± 2.16 mm and 36.11 ± 2.40 mm, respectively, in Sep 2002, 31.75 ± 2.38 mm and 34.52 ± 3.94 mm, respectively, in Oct 2002, and in Dec 2001 30.83 ± 2.11 mm and 32.33 ± 1.84 mm, respectively. Males and females were at a maximum length of 36.7 ± 2.33 mm and 37.2 ± 1.85 mm, respectively in Nov 2001 and at a minimum of 30.8 ± 1.61 mm and 30.2 ± 1.27 mm, respectively in July 2002. The mean adult length over one year was 34.1 ± 3.87 mm, with a midline pronotal length of 7.8 ± 0.31 mm (data not shown).

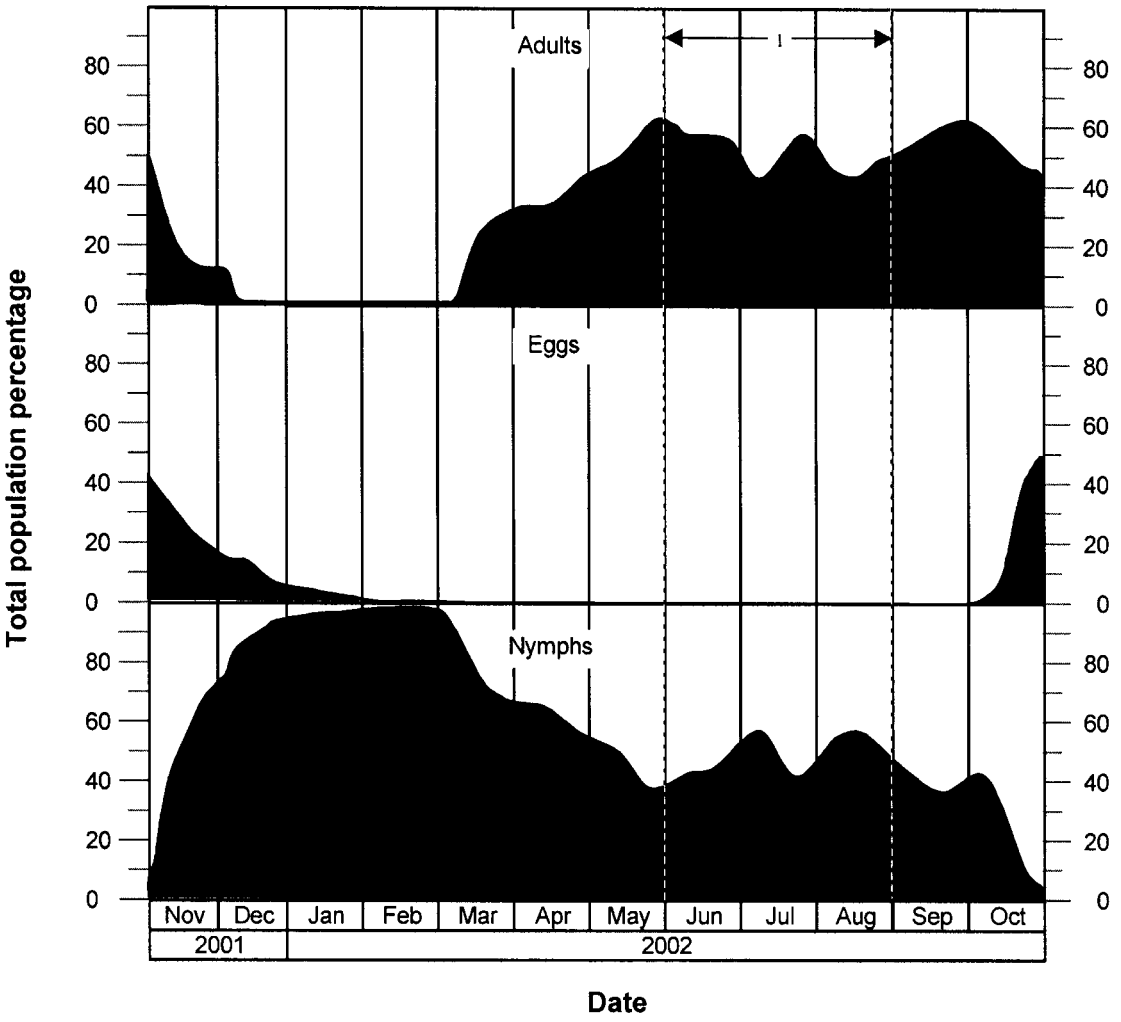

Fig. 1 The ontogenic stage population percentage of *Gryllotalpa africana* at Pretoria Country Club, Pretoria, South Africa from November 2001 to October 2002. Winter period.

Pronotal length was within the ranges reported by Townsend (1983). Development may be measured by other parameters than total length, but this study is also concerned with management, where a total length measurement is more practical and easily interpreted by turf managers. Management related sizes for other mole cricket species have also been reported in total length (Potter 1998; Brandenburg & Williams 1993).

Table 1 summarizes female reproductive activity and the sex ratio of *G. africana* per month over an annual period. Female oocytes started to develop in Apr and the percentage females with oocytes peaked in the winter months (Table 1). During Jul 2002, 92.3 ± 10.13% of females contained oocytes, a figure which was 20.0 ± 42.16% in Dec 2001. The mean percentage oocytes per female was highly variable in Dec 2001, but appeared to fit a declining pattern. Oocytes smaller than one mm in length were found in females from Apr 2002 to Aug 2002 they increased to 1.5-2.0 mm in Sept 2002 and 2.0-2.5 mm during Oct 2002, Nov 2001 and Dec 2001 (data not shown). Females containing eggs (2.5 mm to 3.5 mm long) were sampled regularly in Sep 2002, Oct 2002, Nov 2001 and Dec 2001, but peaked in Oct 2002 at 43.0 ± 0.00% of the female population. The highest number of internal eggs per female was found in Sep 2002 (38.4 ± 8.55), progressively declining to Dec 2001 (12.3 ± 9.78). The significance level for each sample was calculated as $P > 0.00217$ ($P > 0.05/23$ comparisons). Table 1 summarizes the mean (± SD) monthly percentage males of the adult population over 12 months. The adult field sex ratio was male biased one sampling date in May 2002 (date 1: 82.22% males, $P > 0.00002$, N = 45, date 2: 51.61% males, $P > 0.89908$, N = 62). Female bias (in the adult population) was found in

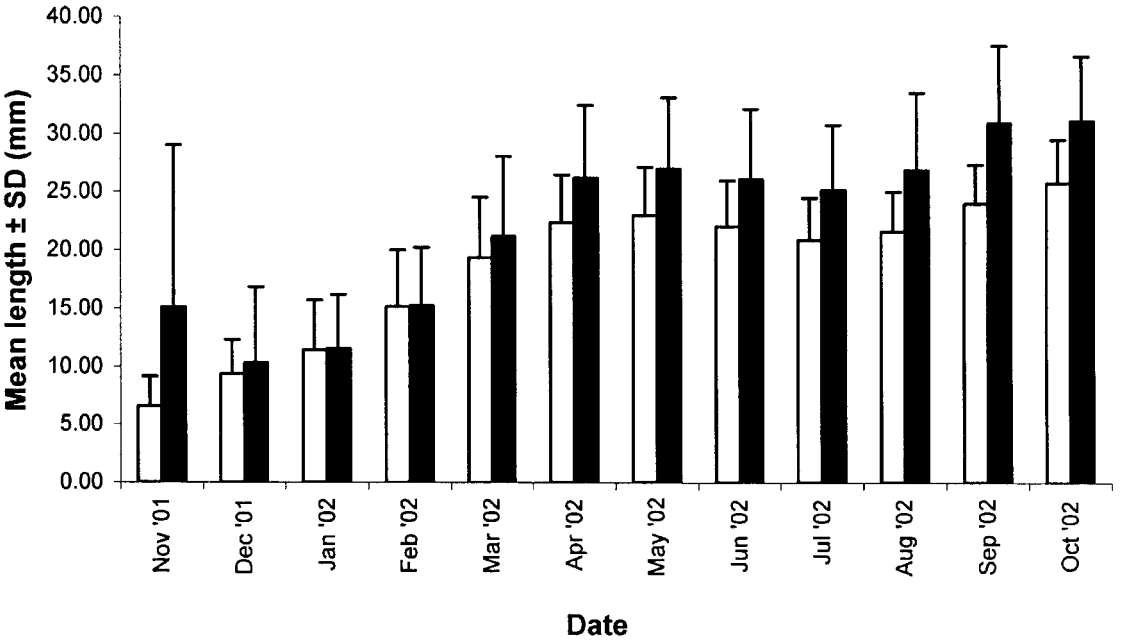

Fig. 2 The monthly mean total length (± SD) (from the posterior of the abdomen (excluding cerci) to the distal end of the labrum) of the nymph and total (adult + immature) population of *Gryllotalpa africana* at Pretoria Country Club, Pretoria, South Africa from November 2001 to October 2002. Total = black, nymphs = white.

both Aug 2002 samples (date 1: 12.12% males, $P > 0.00001$, N = 33, date 2: 24.53% males, $P > 0.00027$, N = 53). The first Sep 2002 adult sample was also female biased (date 1: 25% males, $P > 0.00023$, N = 56, date 2: 30.65% males, $P > 0.00316$, N = 62). The statistical results also indicated a female bias for the first Oct 2002 adult sample (date 1: 18.87% males, $P > 0.00001$, N = 53, date 2: 27.5% males, $P > 0.00643$, N = 40).

Field (Table 1) sex ratio data (as a male percentage, respectively) were normally distributed in the linear scale (Sokal & Rohlf 1997) for comparable months (Kolmogorov-Smirnov test, $P > 0.05$) ("Statistica" Version: 5 (Statsoft, Inc. 1995)).

Discussion

During the study period, vitellogenesis was observed from Sep and *G. africana* females laid fertilized eggs from Oct (mid spring). The highest number of fertilized eggs in the field was calculated as occurring during the end of Oct with some fertilized eggs laid until early Mar. Oviposition was in clutches (pers. obs.) but the subterranean nature of egg laying and clutches per female are unknown. The number of eggs per female and the adult population started declining from late Sep and reached a minimum in mid Dec (early summer). The monthly spring oviposition period was characterized by the longest females over an annual period that also comprised a significant proportion of the adult population. Female abdomen length appeared to increase with egg containment, as females were on average longer than males only at this time. However, female abdomen length did not appear to be linearly related to egg numbers. Absolute length may therefore not be the best measure to quantify adult size. Gender behavioral changes may also have influenced sampling results (lengths) over this period, but were assumed not to cause significant prejudice.

The data suggest mortality among males was high during late winter/early spring (causing a female bias). Migration through flight was not responsible for temporal gender bias in the field, as the monthly flight sex ratio was not significantly different to the monthly field sex ratio and also showed similar patterns. High male mortality after mating has been reported for other mole crickets (*Scapteriscus* spp.) with a univoltine life cycle (Brandenburg & Williams 1993; Buss et al. 2002), which suggests, if *G. africana* males show a similar tendency, that mating of *G. africana* occurred before spring in the present study. Mating may have occurred in autumn, which has been reported for univoltine *S. borellii* (Walker & Nation 1982), which also oviposit during spring (Frank et al. 1998). Further research (examining female spermathecae for sperm) will confirm mating period(s). The majority of adults were presumed dead (none recovered by soap flushing from the soil) by Dec (early summer), when the sex ratio approached 60:40. This suggests that high female mortality occurred after the oviposition period as reported for

TABLE 1. ADULT FEMALES CONTAINING IMMATURE AND MATURE OOCYTES (EGGS) (AS A FEMALE POPULATION PERCENTAGE, RESPECTIVELY), EGGS PER ADULT FEMALE AND THE ADULT SEX RATIO (AS THE PERCENTAGE MALES OF THE ADULT POPULATION) OF *G. africana* AT PRETORIA COUNTRY CLUB, PRETORIA, SOUTH AFRICA FROM NOV 2001 TO OCT 2002. (IMMATURE OOCYTES <2.5 MM AND MATURE OOCYTES (EGGS) >2.5 MM).

Date	Percentage females containing oocytes (mean ± SD)	Percentage females containing eggs (mean ± SD) (number of eggs per female) (mean ± SD)	Percentage males in population (mean ± SD)
November 2001	51.9 ± 16.94	35.71 ± 12.83 (23.4 ± 8.20)	36.1 ± 1.78
December 2001	20.0 ± 42.16	40.0 ± 21.09 (12.3 ± 9.78)	40.0 ± 16.24
January 2002	No females	No females	100 [a]
February 2002	No females	No females	100 [a]
March 2002	0.0	0.0 (0.0)	65.5 ± 11.92
April 2002	22.1 ± 14.67	0.0 (0.0)	53.0 ± 5.08
May 2002	36.6 ± 7.11	0.0 (0.0)	64.5 ± 15.18*
June 2002	91.8 ± 7.06	0.0 (0.0)	50.5 ± 0.63
July 2002	92.3 ± 10.13	0.0 (0.0)	36.6 ± 9.32
August 2002	80.0 ± 17.58	0.0 (0.0)	19.8 ± 6.07*
September 2002	62.7 ± 3.87	32.7 ± 8.60 (38.4 ± 8.55)	28.0 ± 2.83*
October 2002	45.6 ± 7.95	43.0 ± 0.00 (31.3 ± 9.15)	22.58 ± 0.04*

[a]Only one male and no females sampled (insufficient number for an inference).
*$P < 0.001$ in at least one sample (see results) (Two tailed binomial distribution, Bonferroni correction ($P = 0.05/23 = 0.002$)).

other mole crickets with a univoltine life cycle (Brandenburg & Williams 1993; Buss et al. 2002).

Eclosion (egg hatch) began in November, when distinctive first and second instars were abundant, and continued up to mid March. First instars were dorsally black with thin, white, horizontal, abdominal stripes, apterous and from personal observations, were the only active jumpers. Their total length was approximately 7 mm. Second instars were dorsally brown, apterous and up to 9 mm total length. All following instars were dorsally greyish-brown (adults and nymphs are light yellow on the ventral side) and resembled adults in appearance but were smaller and only developed wing buds in later instars. The relatively long oviposition period caused some instar overlap, as evident from standard deviation values for mean nymph absolute length. The overall (adult and nymph) mean absolute length was highly variable in November, but length was shorter with less variability in December, as a result of adult mortality over the two months. Nymphal development rate increased with relative warmer temperatures and the new generation adults appeared from late summer/early autumn. Adults have fully developed tegmina and hind wings and are capable of flight. The new generation adults consisted of more males during autumn, with a significant male inclination in May (although May samples were subject to relatively high variance). This suggests that males may eclose before females and then subsequently die earlier. The data indicate a minimum period of five months from oviposition to adult. The life cycle may, however, have been as long as eight or nine months if oviposition took place in late summer. The seasonal ontogenic stage occurrence was relatively similar in flush samples from across the Pretoria region (unpublished data).

Most nymphs completed their development by early June, when an over wintering phase was entered to the end of August, during which time individuals may have moved deeper down in the soil profile. During this period, small, patchy infestations (lowest density sampled during late July) were found in moist turf areas with relatively high soil temperatures (usually northern exposures). Sampling bias may have caused relatively high variability in life stage constitution during over wintering. Factors including behavioral changes, relative smaller samples prone to higher variability and/or destructive sampling may have contributed to the bias. Total length during winter samples showed a relative decline and also may have been due to sampling bias. Smaller (in relation to length) individuals sampled may have reflected a tendency of younger (and shorter) adults and nymphs to stay active as long as possible to attain a larger size (longer length) to increase their fitness during the following spring reproductive period. Larger males of *Scapteriscus* spp. produce louder calls and attract more females (Forrest 1980, 1983, 1991), while larger *Scapteriscus* spp. females produce three times more offspring and 1.5 times as many eggs per clutch than smaller females (Forrest 1986). The *G. africana* population became more adult biased during spring, when the development was completed. Adult length during spring was variable by month, but may support a contention by Forrest (1987), that as the spring reproductive period season progresses, a greater proportion of smaller individuals (of both genders) should mature because costs due to delaying reproduction increase.

There was annual variation (on a constant spatial scale) in the development of *G. africana*. Mean egg hatch in 2002 was 2 weeks later than in 2001. Soap flushes should, therefore, be con-

ducted weekly to quantify spatial and temporal variance (this is especially important to guide management practices).

The seasonal development of *G. africana* reported in this study is very similar to that reported for univoltine *Scapteriscus* spp. in the southeastern U.S.A. (Brandenburg & Williams 1993).

Preliminary studies indicate peak oviposition occurred a few weeks later on golf courses in the cooler, southern regions (Johannesburg), a pattern followed by some New World species (Brandenburg 1997; Potter 1998). Temperature therefore appeared to be an important factor influencing egg laying period in *G. africana*. Brandenburg (1997), however, found that timing and intensity of egg-laying and egg hatch do not seem to be closely related to soil temperature or the number of *S. vicinus* and *S. borellii* females captured in acoustic traps. Hertl et al. (2001) found a significant positive linear relationship between ovipositing females (number of eggs laid per female were constant) and soil moisture in *S. borellii*. Soil moisture may also influence oviposition in *G. africana*.

Preliminary studies also show that the proportion of adults in the population prior to overwintering might be smaller in the southern areas (Johannesburg). Adult overwintering proportions are variable (on a constant spatial scale) for *S. vicinus* (Brandenburg 1997), suggesting that values reported in this study may also be variable between years.

Some specific behaviors of *G. africana* were observed during the course of this study. Adults were found to be cannibalistic, especially at high densities. *G. africana* adults usually expelled a characteristic non-sticky, pungent smelling, dark brown fluid when handled, possibly as a deterrence or defense mechanism (pers. obs.). Other genera (*Neocurtilla* and *Scapteriscus*) and *Gryllotalpa* species (*G. oya*) also are known for secreting fluids that may be smelly and vary from a low to high viscosity (Baumgartner 1910; Tindale 1928; Walker & Masaki 1989).

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