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ANNUAL ACTIVITY PATTERNS OF THE AUSTRALIAN TARANTULA *SELENOCOSMIA STIRLINGI* (ARANEAE, THERAPHOSIDAE) IN AN ARID AREA

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ABSTRACT

Activity patterns of a population of the burrow-dwelling theraphosid spider, *Selenocosmia stirlingi* Hogg, at Coombah (N.S.W.) are reported. Burrows were located and monitored at about 6-weekly intervals over a period of 3 years while rainfall and diurnal temperature profiles of the soil were also recorded. Spider activity was determined both from the condition of the burrow entrance and from the presence of the spider at the burrow entrance during the night. Activity was greatest in spring and late summer/fall, with low levels of activity in both winter and mid-summer. It is likely that the temperature profile in the soil was exploited behaviorally by the spiders in order to thermoregulate. Estimated losses of spiders from the population were greatest in spring and early summer, and may be due predominantly to maturing males leaving their burrows in search of females.

INTRODUCTION

Stradling (1978) determined that the tarantula *Avicularia avicularia* Linnaeus matured in 3-4 years in the tropical conditions of Trinidad, compared to a projected development period of 10 years for an arid zone species, *Dugsiella hentzi* (Girand), in Arizona (Baerg 1958). Stradling's (1978) data showed that the variation in size increase and instar duration increased as the spiders grew. It therefore seemed likely that environmental factors, such as food availability (e.g., Turnbull 1962, 1965), temperature (e.g., Peck & Whitcomb 1970) and photoperiod (Peck & Whitcomb 1970) might cause these accumulated differences.

In Australia, *Selenocosmia stirlingi* Hogg occurs throughout arid areas in the center of the continent, and its range extends into northern tropical regions (Main 1964). The environmental variation across its range suggested that it would be an appropriate candidate for the investigation of phenotypic plasticity in growth and development. Investigations of the field ecology of *S. stirlingi* formed part of a broader study of the influence of environmental factors on the spider's growth and development (Kotzman 1986). The field study described here was undertaken to characterize the arid environment in which these spiders live (particularly in terms of temperature) and to establish the spiders' natural activity patterns in the context of these conditions. As these spiders occupy deep burrows and forage nocturnally from the burrow entrance, "activity" was measured by

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indications of the spider's use of the burrow entrance. Diurnal variations in soil temperatures were recorded, rainfall records were obtained from the nearby homestead, and the condition of marked burrows and activities of their occupants were monitored. From these observations, a general picture of the relationships between the activities of the spiders and the changing environmental conditions was derived.

STUDY AREA AND METHODS

Distribution of *S. stirlingi* is patchy, and only after thorough searching was a study site chosen (about 180 × 450 m) about 5 km south of the Coombah homestead, on the east side of the Silver City Highway 136 km north of Wentworth (New South Wales). The site consisted of a central swale bordered on the north and south by sandhills, and to the east by a claypan, with a total relief of about 7 m (Fig. 1). Ground cover varied enormously during the study, from virtually none to dense grasses and herbs. In general, vegetation of the area is described as a Belah-rosewood community, including scattered trees (*Casuarina* sp.) about 100 m apart, with "blue bush", herbs and grasses beneath (Cunningham et al. 1981). During each visit, at approximately 6-week intervals, new burrows were located by systematically searching the length and breadth of the field site. Each new burrow was marked with a wooden stake (placed 150 mm west of the burrow) and numbered sequentially as it was found. The condition of all burrow entrances was assessed and the presence or absence of the spider (and juveniles) at the entrance at night was noted. Burrow diameter was measured to the nearest mm using a dial caliper (Mitutoyo Co.) and depth was determined to the nearest cm by inserting a length of rubber into the burrow. In a nearby area, fifteen burrows were excavated to determine their structure and to collect spiders for laboratory experiments.

A planimetric map of burrows and other major features in the site was produced with a telescopic level (Fuji Corp.) and a pair of plane tables. Spot heights were measured along a series of levelled transects and the contours interpolated between them were converted to altitudes above sea level using a Special Survey mark (SSM 3910, 33°01′ South, 141°38′ East) located within the site. The distribution of burrows within the site was compared with the values expected with a low frequency, discrete, random distribution (Poisson) and a coefficient of dispersion (*C.D.*) was calculated (Sokal & Rohlf 1969).

Rainfall data were obtained from a plastic wedge rain-gauge at the Coombah Homestead (5 km north of the field site). Solid state temperature sensors (AD590JH) connected to a 4-channel Rustrak™ recorder (Galton Inc., U.S.A.) were used to monitor field temperatures for 24 h during each visit. Initially two sensors were buried at 25 and 60 cm and allowed to equilibrate for 6 weeks. The temperatures recorded with buried sensors were the same as those from sensors at similar depths within burrows. Therefore, sensors were buried at the surface, 20 cm and 60 cm for the remainder of the study to determine burrow temperatures.

Spider activity was assessed in terms of the burrow entrance condition ("open" or "closed") and the presence or absence of the spider (and any juveniles) in the top of the burrow at night ("seen" or "not seen"). Evidence of the seasonality of male mate-seeking activity was obtained from the records accompanying the 16 male specimens of *S. stirlingi* held in the South Australian Museum, one

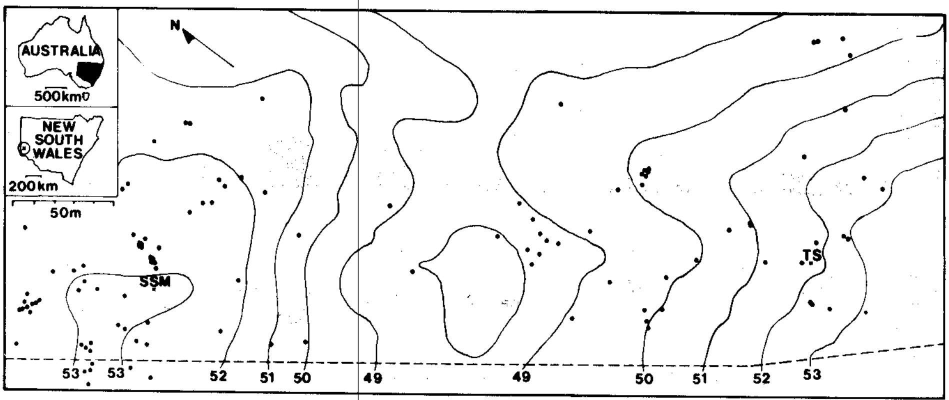

Figure 1.—Location and map of the field study site at Coombah (N.S.W.): spider burrows (dots), 1 m contours (solid lines, heights above sea level), roadside fenceline (broken line), buried temperature sensors (TS) and Special Survey Mark (SSM).

specimen collected at the Coombah Homestead during the study, and the type specimen from the British Museum (Natural History).

RESULTS

Conditions in the field area.—Daily rainfall records were combined to produce monthly totals (Fig. 2). Average annual rainfall during the study ranged from 130.0-408.3 mm, with no rain falling in 10 of the 37 months. The rainfall pattern observed during the study was typical of this region and compared well with longer-term figures from Menindee (100 km northeast of Coombah) where annual falls have ranged from 52-766 mm and the mean is 236 mm (Cunningham et al. 1981). At Coombah the mean annual rainfall over the 3 years was 232 mm, and thus biotic activity related to rainfall (including spider activity) can be considered typical of the area.

The diurnal temperature ranges were greatest at the soil surface (up to 45° C), less at 20 cm (typically 5-7° C) and least at 60 cm (no more than 2° C) (Fig. 2). The trends for annual ranges were the same. Summer temperatures at the surface were 15-50° C, at 20 cm 25-32° C and at 60 cm around 25-30° C. Winter temperatures at the surface were 10-30° C, at 20 cm 12-22° C and at 60 cm about 15° C. The slow transfer of heat through the soil caused the maxima and minima to be reached 6 hours after the surface at 20 cm and 12 hours after the surface at 60 cm. After dawn, the surface temperature generally increased sharply until noon, whereafter it would oscillate about the maximum until declining steadily after sunset to a pre-dawn minimum. In the soil, temperatures cycled evenly between daily maxima and minima.

Burrow characteristics and distribution.—Burrows of *S. stirlingi* were unbranched and vertical with somewhat enlarged, horizontal chambers at the base and total lengths ranging from 31-100 cm. Some were slightly spiralled or gently curved. Burrow diameter was constant from top to bottom and there was little silk in the walls. The entrance was circular (diameter 15-27 mm) with a slightly "trampled" flange, but no turret, door or collar of silk. Occasionally, a thin film of silk covered the entrance. Although third instar spiderlings raised in the laboratory constructed small burrows (about 5 mm diameter), none less than 15

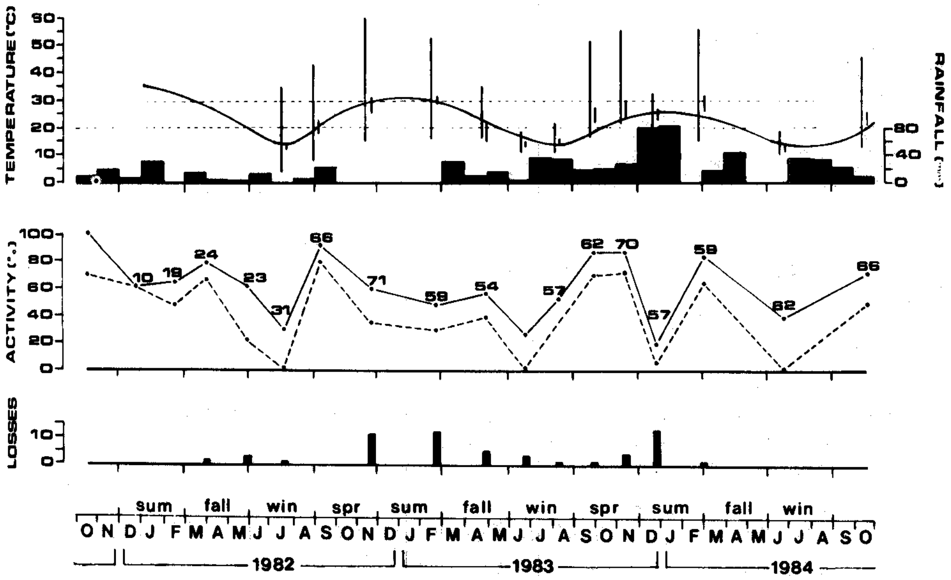

Figure 2.—Environmental conditions and spider activity at Coombah (N.S.W.). Upper: Monthly rainfall totals (solid bars) and diurnal soil temperature ranges: temperatures at 60 cm (+/−1°C diurnally) (solid line), temperature ranges at the surface and 20 cm (pairs of vertical lines) and the temperature range for spider growth (broken lines) (see text). Middle: Adjusted spider activity (see text); the percentage of open burrows (solid line), burrows in which the occupant was seen (broken line) and adjusted population size (*N*). Lower: Number of burrows closed for longer than 260 days indicating spiders lost from the population.

mm diameter was found in the field. Therefore the population which was monitored consisted of half to fully-grown spiders.

At the conclusion of the study, the site (approximately 81,000 m^2) contained 111 marked burrows (mean density = 13.7 burrows/ha). Analysis of the number of burrows in each 100 m^2 revealed that the distribution was not random $\chi^2 = 45.78$, $df = 2$, $p < 0.001$), and that they were clumped (*C.D.* = 2.95) (Sokal & Rohlf 1969) (Fig. 1). Although burrows were scarce near the claypan, no other superficial physical features appeared to be correlated with the distribution of burrows.

There was little correlation between burrow diameter and depth ($r^2 = 0.11$) (Fig. 3). There appeared to be a positive, linear relationship between burrow depth and altitude on the lower slopes (i.e., < 51 m), however, burrow depth appeared to be independent of altitude on the upper slopes (Fig. 4).

Spider activity patterns.—Similar trends of spider activity were observed using two measures: open burrows and those in which spiders were seen at night. Open burrows were those in which spiders were active, or those which were neither plugged by the spider nor closed with sand and debris moved by wind and/or rain, whether the spider was present or absent. Open burrows in which the spiders were not seen may have been recently abandoned, or the spider may have been temporarily out of sight within the burrow. The proportions of spiders seen were generally 10-20% lower than the proportion of open burrows. Activity was low in winter (June-July), peaked in spring (September-November) and early fall (March, April), and was depressed to a variable extent during summer (December-February). Activity data were expected to be unrealistically high in the first 10 months as inactive burrows were generally not found, so only the

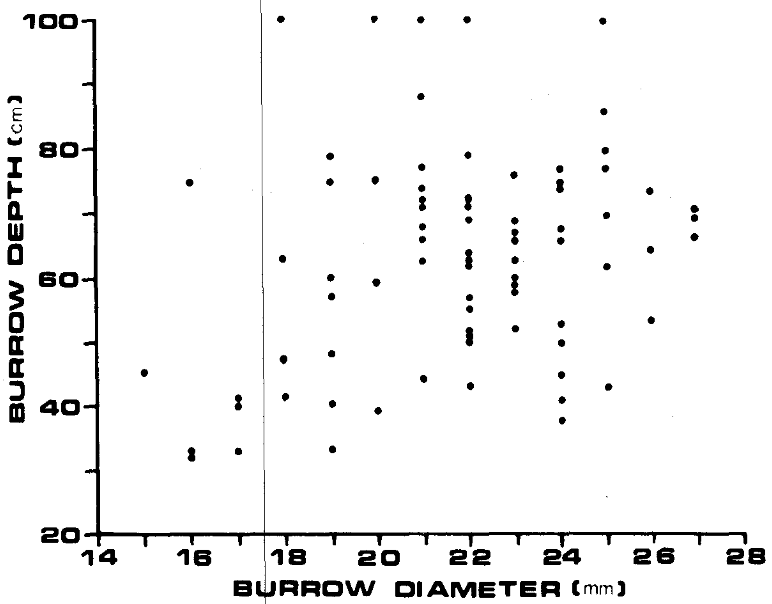

Figure 3.—Relationship between burrow depth and diameter, Coombah (N.S.W. (N = 80, $r^2 = 0.11$).

trends of these data were considered. For the remainder of the study, the absolute percentages of active burrows ranged from 10-85% "open" and 0-75% "seen". As the total number of burrows monitored increased from 72 to 111, the maximum activity levels declined throughout the study to 45% "open" and 35% "seen".

Burrows became blocked from the action of natural agents (such as wind and rain) when the spider did not clear the entrance, or as a result of deliberate plugging by the spider within the top 10-15 cm of the burrow, or both. When

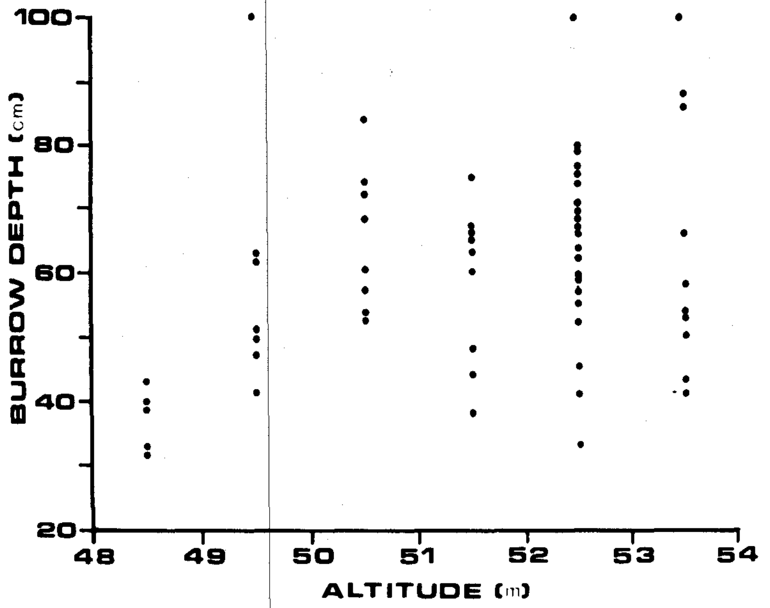

Figure 4.—Relationship between burrow depth and altitude (mid-point between contours), Coombah (New South Wales) ($N = 80$, $r^2 = 0.14$).

burrows were closed, there was usually no evidence of the entrance, and it was generally not possible to determine the cause(s) of closure.

Within 260 days 90.5% of burrows which were inactive became active again. To estimate the losses from the population (from death or dispersal), burrows which remained inactive for periods longer than 260 days were considered to be unoccupied and adjusted activity levels were calculated with the remaining burrows (Fig. 2). While adjusted activity patterns were essentially the same as those obtained with the unadjusted population, the maximum levels were higher at about 90% "open" and 70-80% "seen", in a population ranging from 54-71 burrows. Apparent losses from the population were not uniformly distributed throughout the year, but peaked in summer (Fig. 2).

Small spiderlings (instars II-IV) were seen in December, February and March, indicating egg production in spring and summer. Males usually wandered outside the burrows in March and April (although two were collected as late as June). Together, these observations suggested that molting occurred in late summer and mating from summer through winter.

DISCUSSION

Burrow characteristics.—A high correlation between spider size and burrow diameter has been demonstrated in some burrowing spiders (Decae et al. 1982; Miller & Miller 1984). Petrunkevitch (1911) also suggested that larger spiders should occupy deeper burrows having had longer to dig them. The burrow depth of *S. stirlingi* was independent of burrow diameter (Fig. 3) suggesting that either variable growth was producing different-aged spiders of similar sizes, or that other factors, such as soil moisture or texture, affect burrow depth. The increase in burrow depth with increasing altitude up to 51 m provides circumstantial support for the potential importance of both soil moisture and texture. The formation and maintenance of the sand dunes by the action of wind and water (Bowler 1980) results in the progressive downslope accumulation of clays (Leeper 1964), and potentially an inverse relationship between altitude and soil moisture owing to the water-holding properties of clays. In addition, calcareous layers may form within the dune when the water table recedes (Bowler 1980). Meat ants, *Iridomyrmex purpureus* (Sm.), whose nests are abundant in this area, penetrate these layers as a defense against moisture and thermal stresses and to avoid nest predation (Ettershank 1971). While *S. stirlingi* may use a similar strategy, extensive excavation of burrows would be necessary to clarify this possibility.

Burrow blocking behavior.—The closure of burrows at different times of the year may have different causes. Like other theraphosids, *S. stirlingi* sometimes made burrow plugs by combining sand and web (Gertsch 1949; Minch 1979a). Alternatively, some burrow entrances appeared to become blocked by the natural accumulation of sand and debris as with the wolf spider *Geolycosa wrightii* (Emerton) (Gwynne & Watkiss 1975). Main (1978) and Gray (1968) recorded door-sealing behavior of trapdoor spiders associated with seasonal weather conditions and predator avoidance. For *S. stirlingi*, it seems likely that deliberate plugging was probably most common in summer (providing protection during molting and egg production), while natural weathering may have predominated in winter when spiders were inactive in the cold conditions.

The origin of newly-located burrows is difficult to explain. It seems unlikely that they were new burrows of spiders already in the population or new adult recruits from outside the area as there were never sufficient tailings to indicate excavation of an entirely new burrow. It seems most likely that they were juvenile recruits which had reached sufficient size to be detected (since no burrows smaller than 15 mm were found), and/or existing large burrows which had opened after prolonged periods of closure.

Losses from the population were estimated on the basis of unusually prolonged or continued burrow closure. Spiders may have died due to old age or disease, during molting (as often observed in the laboratory), following attack by parasitic wasps, or they may have dispersed. No evidence was found to suggest that burrows were vacated in favor of new dwellings. However, if spiders dispersed to existing burrows, such activity would still have been recorded as a loss. Molting, mating and production of young in other species of theraphosids are summer activities (Baerg 1958; Minch 1979b), and adult *S. stirlingi* maintained in the laboratory also molted at this time. As the timing of losses coincided with the production of young at Coombah, it seems likely that mid-summer losses may have represented the maturation and departure of males for the following breeding season. Deaths associated with molting would also tend to predominate in summer.

Spider activity.—The potential for growth can be used to relate activity at the burrow entrance with temperatures in the soil. In laboratory studies, rates of growth and development (mediated by food availability) were maximized at 29° C, decreased linearly from 29-25° C and ceased at and below 20° C (Kotzman 1986). At 60 cm within the burrow, 20° C was exceeded only from September through May and 29° C reached only in mid-summer. As the highest levels of activity were recorded consistently in September and October, the spiders probably exploited elevated temperatures near the burrow entrance. Humphreys (1974) recorded almost constant body temperatures in the burrowing wolf spider *Geolycosa goderffroyi* (L. Koch) achieved by behavioral thermoregulation. Similar behavioral adjustment of body temperature in *S. stirlingi* could facilitate feeding, growth and development by allowing the spider to optimize its body temperature for these activities: nocturnal foraging during spring and fall (necessarily near the surface), feeding (anywhere within the burrow), and molting or egg laying in summer (in the chamber at the base of the burrow).

The spring peak of open burrows corresponded to the time when the burrow temperature increased above 20° C and daylength was increasing. Minch (1979b) claimed that temperature was not the cue for burrow unblocking in *Aphonopelma chalcodes* Chamberlin, as spiders at different altitudes (and hence temperatures) opened their burrows at virtually the same time. In addition, he observed that spiders maintained in the laboratory blocked their burrows somewhat later than those in the field, and suggested that photoperiod or temperature might at least moderate the behavior. As both temperature and photoperiod are increasing in spring, it would be difficult to uncouple these factors under field conditions. While it is possible that annual activity patterns may be controlled by an endogenous clock set genetically or during early development (Minch 1979b), it seems more likely that the transition past a temperature limit (Gabel 1972) regulates burrow-blocking behavior through its connection with growth processes.

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