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THE NATURAL HISTORY OF THE CALIFORNIA TURRET SPIDER *ATYPOIDES RIVERSI* (ARANEAE, ANTRODIAETIDAE): DEMOGRAPHICS, GROWTH RATES, SURVIVORSHIP, AND LONGEVITY

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ABSTRACT. A large and dense population of over 500 burrows of *Atypoides riversi* in a 2.0 × 3.2 m area was monitored for two years to indirectly determine demographics, growth rates, survivorship and longevity of the spiders. Twelve size classes of spiders were designated by correlating spider size to burrow size. All size classes were present simultaneously throughout the year. Variable growth rates were recorded for spiders in each size class, and survivorship was lowest for spiders in the smallest size classes. It is estimated, based in large part on growth rates, that *A. riversi* can live at least 16 years in the field.

The only long term comprehensive study of the genealogy and demography of a large population of mygalomorph spiders concerns the Australian ctenizid *Anidiops villosus* (Rainbow) (Main 1978). In another study, Marples & Marples (1972) observed a population of several species of New Zealand ctenizids for six years. The demographics of burrowing wolf spiders have been examined in detail by McQueen (1978, 1983), Humphreys (1976) and Miller & Miller (1991).

Herein I describe the natural history of the fossorial mygalomorph spider *Atypoides riversi* O. P- Cambridge, the California turret building spider (Rivers 1892). Unlike the long term field studies of Main and the Marples, my objectives were to determine, in a two-year period, the demographics, growth rate, survivorship, and longevity of *A. riversi*. Unlike Main (1978) and Marples & Marples (1972), who measured burrow and door diameters but did not correlate these measurements to spider size, I measured and correlated burrow entrance size to spider size. McQueen (1978), Humphreys (1976) and Miller & Miller (1984) found positive correlations for certain burrowing wolf spiders. Decae et al. (1982), studying the burrow structure of a ctenizid, also found a positive correlation between carapace length and burrow diameter but did not associate this with longevity. Using the correlation and following all burrow size changes through the two year period, I derived life history information comparable to following a single cohort of *A. riversi* through its long life. Miller & Miller (1991) used a similar approach to study *Geolycosa turricola*.

Additional natural history information on various antrodiaetids can be found in Atkinson (1886a, 1886b), Coyle (1971, 1986), Rivers (1891), Smith (1908), Vincent (1980, 1985, 1986), and Vincent & Rack (1982).

METHODS

Study sites.—Two study sites at the University of California's Blodgett Forest Research Station, located in the American River watershed on the western slope of the Sierra Nevada in El Dorado County, approximately 10 miles west of Georgetown and at an elevation 1275 m were chosen for their high density of burrows and uniform ground cover. The population dynamics of spiders in both areas were similar; therefore, this paper reports on only one. Population data for the other study area and vegetation descriptions for both are in Vincent (1980).

The study site measured 2.0 × 3.2 m and consisted of 160 20 cm square quadrats formed by a grid system composed of nylon string and wooden stakes. The stakes were placed at 20 cm increments around the perimeter of the plot, and string was placed on or slightly above the ground connecting facing stakes. Ground cover was mostly pine and cedar needles with occasional pine seedlings present during the spring and summer months. A barbed-wire fence enclosed the study area to exclude deer and other large animals.

Correlation of spider size and burrow entrance size.—A series of 15 non-metric ball bearings ranging in diameter from 2/32 inch (1.59 mm) to 16/32 inch (12.7 mm) in increments of 1/32 inch (0.79 mm) were hard-soldered to thin single fiber wire "handles". These ball bearings were then used to measure the internal diameter of spider burrow entrances. The internal diameter was considered equivalent to the diameter of the ball bearing that fit (or came the closest to fitting) the narrowest section of the tapered burrow entrance. For convenience, burrow size classes were designated by the numerators that fit the entrances (sizes 2–16). Attempts to measure burrow entrances accurately with a caliper or ruler proved to be difficult and damaging to the flexible and fragile entrance.

Six to 14 burrows (n = 128) representing each size class were arbitrarily chosen near the study site for measurement (Vincent 1980). After each burrow was measured, the resident spider was dug from its burrow, anesthetized by cooling with crushed ice (large spiders) or CO_2 (small spiders), and measured. Spiders were measured with a stereomicroscope fitted with an ocular micrometer accurate to 0.039 mm. Measurements of maximum width of both the carapace and sternum were correlated to the internal diameter of the burrow entrance.

Observation platform.—A portable observation platform consisting of a 2 × 1.33 m sheet of plywood was supported approximately 12 cm over the plot by planks and blocks. The leading edge of the platform coincided with the trailing edge of the row being examined to allow a detailed view of one 20 cm square quadrat. After examining all quadrats in a row, I advanced the platform to the trailing edge of the next row, etc. Since *A. riversi,* like some other fossorial mygalomorphs, is sensitive to vibrations, successful observations necessitated moving slowly on the platform. Adjusting the platform caused some spiders to retreat temporarily down their burrows.

Burrow observations.—The position of each burrow was noted and its entrance diameter was measured. Burrows with flexible and freshly silked turrets were measured for size class designation. The following burrow conditions were recorded: (1) occupied [spider was seen in its burrow]; (2) abandoned [burrow appeared in use, but no spider was detected during the immediate observation period, approximately five minutes]; (3) closed [entrance was folded closed and sealed with silk]; (4) missing [burrow could not be found]; (5) old [burrow was in a state of disrepair, the turret was stiff and/or torn or non-existent]. These and other relatively rare burrow conditions are discussed in detail in Vincent (1980).

Data collection dates.—Burrows were initially censused 5–23 September 1976. On 22–24 April 1977 new burrows and burrow conditions for a random sample (n = 153) of previously censused burrows of sizes 3 through 11 were recorded. Also, burrow conditions for all burrows of sizes 12, 13, and 14 were recorded (n = 13). The random-sample size for each size class was determined so that the standard deviation of the estimated proportion would be no greater than 0.30. Confidence intervals for the true proportions were calculated by a formula given in Bickel & Daksun (1977, formula 5.1.13), and modified to account for sampling without replacement (Cochran 1977, sec. 2.15). During 28–31 July 1977, new burrows were mapped and recorded, and previously recorded burrows were measured again. On 20 August 1977 a random sample of burrows present on 28–31 July, 1977 was censused to confirm the presence of spiders in the burrows previously sized. Sample size and confidence intervals were determined as above for the April 1977 random sample. All burrows present on 28–31 July 1977 were recensused 19–20 May 1978 to see if they contained spiders. Burrows that contained spiders on 19–20 May 1978 were recensused and remeasured 3–6 August 1978, and all burrows in odd-numbered rows were observed at night with a dim unfiltered flashlight as a further check on spider presence. If a spider was not immediately visible in its burrow, I waited several minutes for it to appear; if it still did not appear, I considered the burrow abandoned. Again, all new burrows were recorded and mapped.

Survivorship calculations.—Survivorship of *A. riversi* was indirectly determined by subtracting from the initial number of burrows censused the number of burrows missing or considered "old" during each consecutive census. Survivorship of eggs and emerging spiderlings is unknown.

RESULTS AND DISCUSSION

Correlation of spider size and burrow entrance size.—Burrow entrances ranged from 3/32 inch (2.38 mm) through 14/32 inch (11.06 mm). A regression of spider size (carapace widths) against burrow entrance size was highly significant ($P < 0.001$) (Fig. 1).

Assumptions.—In estimating the following

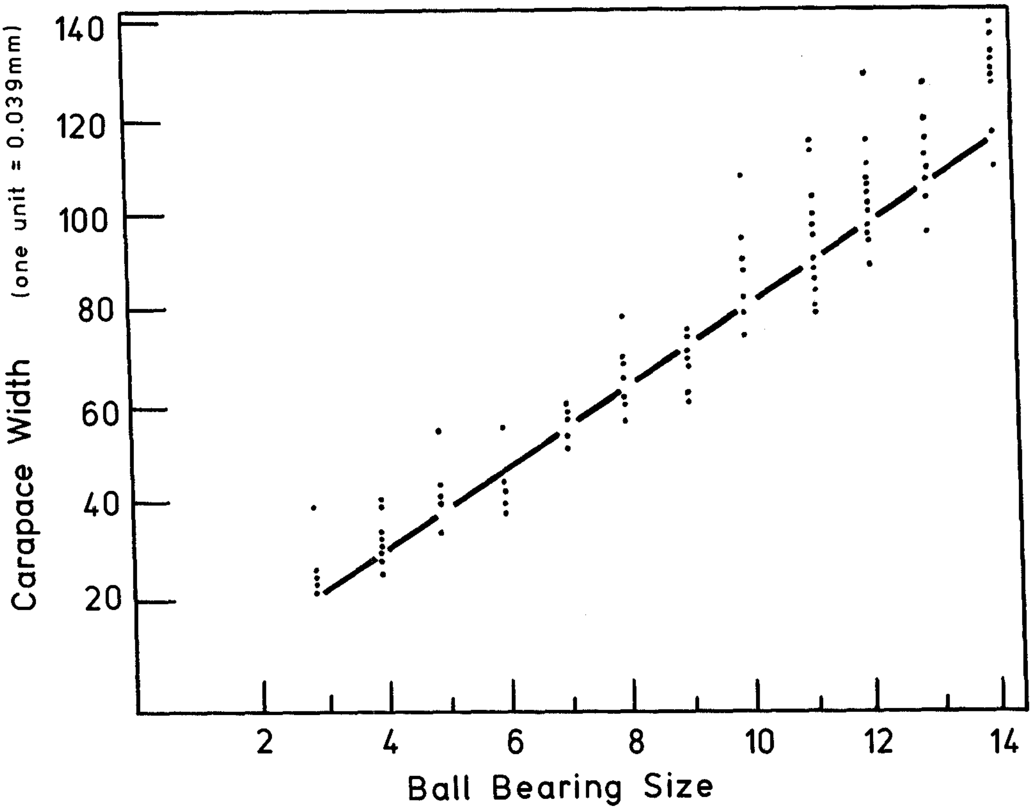

Figure 1.—Regression of ball bearing size on carapace width ($Y = 8.3X - 3.1$, $R^2 = 0.934$, $P < 0.001$).

demographics, survivorship, growth rates and longevity for *A. riversi,* I assume each burrow has had only one occupant who had enlarged and maintained it over time, that burrows present and in good shape contain a living spider, and that missing burrows are a measure of spider mortality.

Various field observations support the assumption of "burrow fidelity". Throughout most of the year I have measured increases in burrow width for all size classes and have often observed excavated soil adjacent to burrows. Further, during hundreds of hours of observing *A. riversi* in the field, only on one occasion was a spider seen totally outside its burrow. (This spider was later found to be parasitized by a nematode). Indeed, the reluctance of *A. riversi* to leave their burrows was evident by the difficulty encountered in coaxing them completely out even with tethered prey; once outside, they rapidly find their way back to their burrow. Additionally, I excavated hundreds of burrows but never found more than one spider in a burrow. Lastly, pitfall traps placed adjacent to or within 25 m of the study sites, during most of 1977, recovered only adult male spiders and only during the fall mating season.

The above observations suggest that *A. riversi* does not leave its burrow to enter another burrow to evict its resident in a competitive interaction (as in Riechert 1978), to search out larger vacated burrows, or to establish new burrows in better areas. Other antrodiaetids (F. A. Coyle & W. Icenogle pers. comm.), all door-building ctenizids (B. Y. Main pers. comm.; Decae et al. 1982), and a burrow-dwelling theraphosid (Kotzman 1990) apparently maintain the same burrow throughout life.

The assumption that burrows which were maintained contained spiders (deteriorated burrows rarely did) was based in part on a 5 August 1978 evening census in which 97.3% of the maintained burrows ($n = 263$) were occupied by spiders. Those burrows in which a spider was not observed at the entrance may still have contained a spider at the bottom, perhaps feeding or repelled by my dim flashlight.

The last assumption equating missing burrows with spider mortality may not be entirely accu-

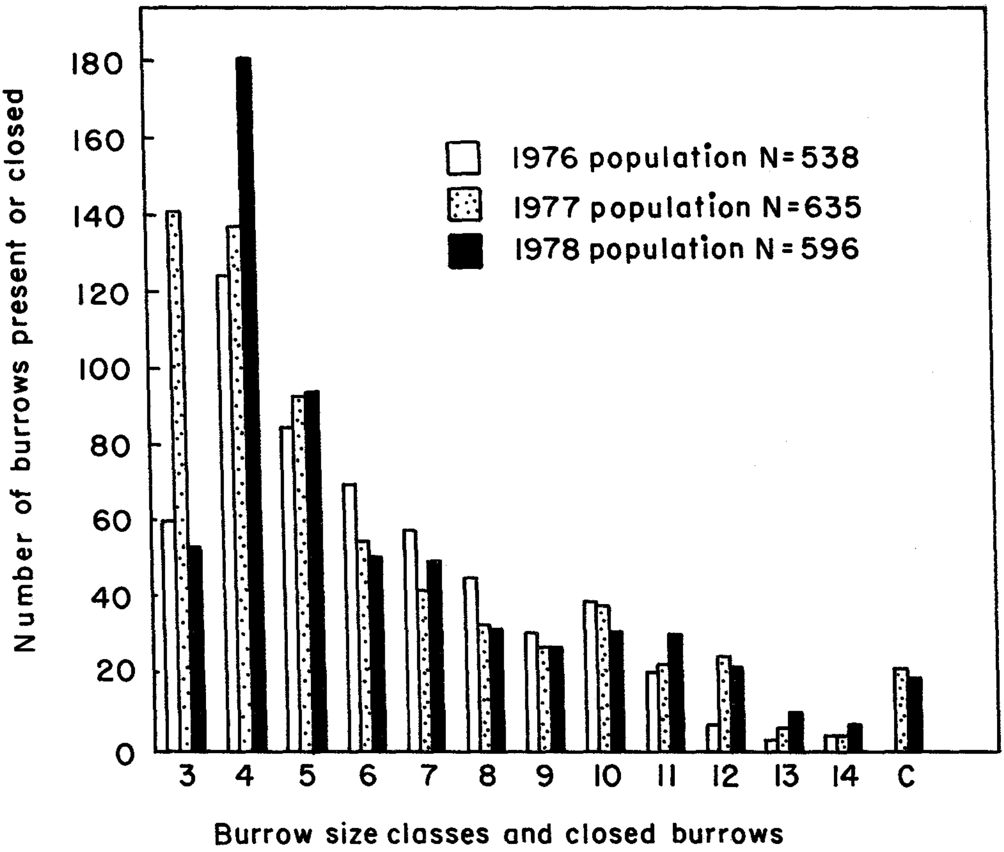

Figure 2.—The number of occupied and closed burrows found for each size class September 1976, July 1977, and August 1978.

rate. In all censuses a few previously unrecorded larger burrows were found. This is most likely indicative of overlooked burrows in the previous census or, less likely, immigration of spiders which had somehow been evicted from their former burrow into the plot. (Some unrecorded new burrows may have been excavated over smaller burrows thus accounting for some of the extreme jumps in size class, as discussed earlier.) If there is some immigration, there may also be come emigration of spiders not detected by pitfall traps or observation. In any case, however, the number of new, larger burrows was small.

Demographics.—Many species of araneomorphs experience a marked seasonality, with certain size classes restricted to specific times of year. All size classes of *A. riversi*, however, occur simultaneously throughout the year. Remarkably high numbers (538, 635, 596) were present for the three years censused (Fig. 2) in densities as high as ten burrows per 20 cm square. Most of the burrows belonged to sub-adult spiders. (Adult females belonged to size classes 11 and above, the only size classes found with eggs or spiderlings; most adult males emerged from size 10 burrows (Vincent 1980)). The July 1977 frequency of burrows in size classes 4–11, 13 and 14 was similar to the September 1976 population (χ^2 = 16.92, *df* = 9, $P < 0.05$), yet close to half the September 1976 burrows increased or decreased in size, and 99 (18.4%) were missing (Table 1). Size classes 5–11, 13 and 14 in August 1978 were similar in frequency (χ^2 = 26.30, *df* = 16, $P < 0.05$) to the September 1976 and July 1977 censuses (Fig. 2). Notably there were fewer size class 3 burrows than size class 4 burrows and fewer size class 9 burrows than size class 10 burrows in 1976 and 1978 (Fig. 2). The large number of size class 3 and/or 4 spiders relative to the smaller number of spiders in the larger size classes indicates heavy early instar mortality, typical of arthropods, for all three years. The

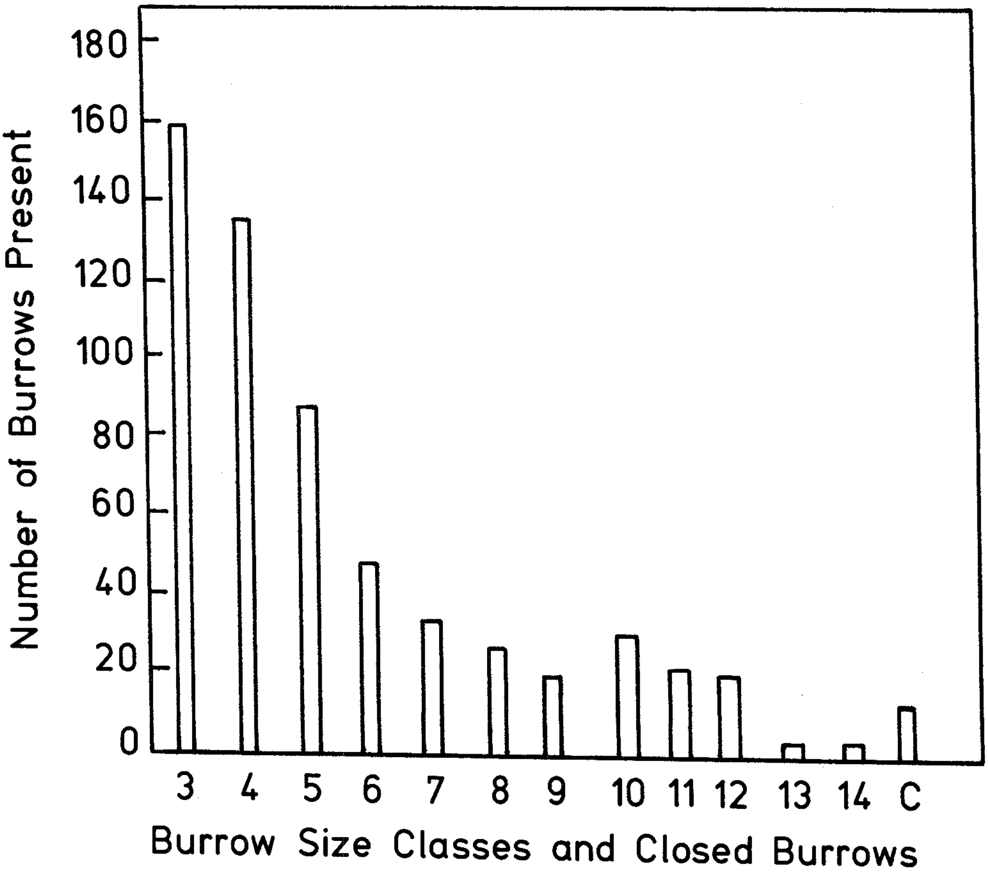

Figure 3.—The number of burrows for each size class occupied by spiders and the number of closed burrows during the May 1978 census.

total numbers of individuals for size classes 3 and 4 varied with time of year, as well as year to year (compare Figs. 2 and 3). However, the large number of new size class 3 and 4 burrows found in April 1977 and May 1978, 205 and 124 respectively, indicate a late fall and/or early spring emergence for spiderlings. This finding is consistent with Coyle's (1971) data. Fewer new burrows of size classes 3 and 4 combined were found July 1977 and August 1978 (40 each) (Vincent 1980).

The drastic decrease in number of size class 3 burrows, the increase in number of size class 4 burrows from May 1978 (Fig. 3) to August 1978 (Fig. 2), and the relatively low number of individuals in size class 3 found in September 1976 (Fig. 2) suggest mortality for size class 3 and/or a transition from size class 3 to a larger size class from the spring to fall. Indeed, of the 187 size class 3 burrows first found April 1977, 59 (31.6%) were missing and 23 (12.3%) grew one size class by July 1977. Of the 87 size class 3 burrows first found May 1978, 10 (11.5%) were missing by August 1978 and 46 (52.9%) grew one size class. The relatively large number of size class 3 burrows found July 1977 compared to August 1978 was a result of the larger number of new size class 3 burrows (187) found April 1977 compared to 87 found May 1978. The number of new spiderlings can be expected to vary extensively, however, as indicated by the range (21–74; $\bar{X} = 46$) in number of eggs produced by nine females adjacent to the study site (Vincent 1980) and a range of 43–80 ($n = 7$) found by Coyle (1971) for a coastal population. Unfortunately, the number and size of clutches within the study site could not be determined. The drop off in numbers of individuals larger than size class 4 (Fig. 2) is due to relatively high mortality (Fig. 4) and growth of size 4 spiders to larger size classes (Tables 1, 2, 3). The more stable distribution of size classes 5 and above appears to have

Table 1.—The total number (*n* and percent (%) of burrows decreasing, not changing, and increasing in size, and those burrows recorded closed or missing in the July 1977 census of burrows first recorded September 1976. "Change" column reflects current burrow status. Other = old, abandoned, or destroyed.

			Size classes as of September 1976											
Change	*n*	%	3	4	5	6	7	8	9	10	11	12	13	14
−3	1	0.2				1								
−2	3	0.6				1	1			1				
−1	30	5.6		1	6	6	6	4		2	2	1	1	1
0	160	29.7	8	57	37	18	13	5	5	8	3	4		2
1	137	25.5	29	32	18	18	13	9	8	4	6			
2	56	10.4	3	3	3	10	7	12	8	8	2			
3	15	2.8				1	5	6	2	1				
4	3	0.6		1		1				1				
6	1	0.2		1										
Closed	20	3.7					3	5	1	5	6			
Missing	99	18.4	16	29	16	12	7	4	5	7	1	1	1	
Other	13	2.4	4		4	1	2		1	1				
Total	538		60	124	84	69	57	45	30	38	20	6	2	3

been maintained by a complex combination of spiders growing at different rates over the same time period and varying mortality rates for spiders in each size class (Tables 1, 2, 3).

Growth rates.—Tables 1 and 2 list changes in burrow sizes and conditions over time for the population of burrows censused September 1976 and recensused July 1977 and the population of burrows as of July 1977 and recensused August 1978. Considering all size classes combined (Fig. 5), the 1976 population had a higher proportion of burrows that did not change size (30%), especially size classes 4 and 5 (Table 1), than the 1977 population (12%).

Most burrows increased one or two size classes in the two year period from September 1976 through August 1978; however a few increased as many as five size classes and some decreased as many as four size classes (Table 3).

Feeding studies in the laboratory (Vincent

Table 2.—The total number (*n*) and percent (%) of burrows decreasing, not changing, and increasing in size, and those burrows recorded closed or missing in the August 1978 census of all occupied burrows as of July 1977; * = other minor changes. "Change" column reflects current burrow status. Other = old, abandoned, or destroyed.

			Size classes as of July 1977											
Change	*n*	%	3	4	5	6	7	8	9	10	11	12	13	14
−5	2	0.3						1		1				
−3	2	0.3					1	1						
−2	6	1.0			3			1			1			1
−1	24	3.9		4	4	1		1	1	4	4	4	1	
0	74	12.5	4	25	13	7	3	3	2	5	7	2	1	2
1	157	25.6	51	39	20	14	5	2	5	7	7	6	1	
2	67	10.9	7	10	16	8	5	9	2	7		3		
3	27	4.4		3	5	5	5	6	1	2				
4	6	1.0		1	3		1	1						
8	1	0.2	1											
Closed	17	2.8	2		1	2	3	2	2	1	2	1	1	
Missing	203	33.1	74	51	23	12	16	5	9	7	1	5		
Other	28	4.5	2	4	4	5	2		4	3		3	1	
Total	614		141	137	92	54	41	32	26	37	22	24	5	3

Table 3.—The total number (*n*) and percent (%) of burrows decreasing, not changing, and increasing in size, and those burrows recorded closed or missing in the August 1978 census of all occupied burrows first recorded September 1976; "Change" column reflects current burrow status. Other = old, abandoned, or destroyed.

			Size classes as of September 1976											
Change	*n*	%	3	4	5	6	7	8	9	10	11	12	13	14
−4	2	0.4					2							
−2	6	1.1			3	3								
−1	13	2.4		3	1	2	3	1		1	1	1		
0	21	3.9	1	5	5	1	2	1		1	2	1		2
1	87	16.2	13	35	12	9	2	4	5	4	2			
2	71	13.2	9	11	16	8	6	6	5	6	3	1		
3	48	8.9	4	8	4	7	8	9	5	2	1			
4	19	3.5		1	2	5	5	5	1					
5	4	0.7		1		1	1	1						
Closed	15	2.8			2	3	4		3	1	1			1
Missing	229	42.6	33	58	37	24	21	15	10	20	8	1	2	
Other	23	4.3		2	2	6	3	3		3	2	2		
Total	538	100.0	60	124	84	69	57	45	30	38	20	6	2	3

1980) revealed that *A. riversi* do molt to smaller or larger sizes depending on food intake. Assuming similar abiotic conditions, the non-uniform growth rate in the field suggests that prey availability or prey capture rates may not always be optimum for some members of this densely packed (up to 635 burrows in a 2.0 × 3.2 m area) population. Perhaps *A. riversi*, like other spiders, molts to a smaller size in the field as a response to starvation to maintain abdominal hydrostatic pressure (Anderson 1974), which is important for locomotion and prey capture (Wilson, 1970).

A non-uniform growth rate may be advantageous to a long-lived species such as *A. riversi* living in dense aggregations. Assuming that maturation of the same clutch is asynchronous, early maturing males would be conducive to outbreeding, especially since adult males appear to die shortly after the mating season (Vincent pers. obs.), whereas adult females live several years in the laboratory and field (presumably with the potential to mate). In this regard, B. Y. Main (pers. comm.) has unpublished data which indicate that males of the long-lived ctenizid *Anidiops* mature a year earlier than females of the same cohort and brood.

Compared to adult females, which continue to molt after maturity (Coyle 1968, 1971), sometimes to larger size class, adult males of *A. riversi* (*n* = 27) had little variability in sternum (2.00–2.36 mm $\bar{X}$ = 2.16, 1 SD = 0.11) and carapace (3.60–4.16 mm, $\bar{X}$ = 3.92, 1 SD = 0.15) measurements, but a wide range of abdominal sizes (as determined by casual observation) both in the field and laboratory. It may be more advantageous for a small penultimate male to sacrifice some abdominal food reserve, which it could have attained by growing another year, to become sexually active sooner (perhaps for a shorter period of time due to a smaller food reserve), than to delay maturation and suffer more exposure to mortality factors.

Survivorship.—Survivorship of *A. riversi* within this study site varied from year to year and within each size class (Fig. 4). Burrows found September 1976 and recensused July 1977 show a gradual increase in survivorship from size class 3 through size class 8 and for size classes 11 and 14. A similar trend for the ctenizid *Anidiops* has been recorded (B. Y. Main pers. comm.). The drop off in survivors for burrows in size classes 9 and 10 probably reflects both male emergence in search of mates, (see "abandoned" burrows (Vincent 1980)), as well as mortality within the burrow (see "missing" burrows, Tables 1, 2, 3). Size class 10 burrows often contained males or were vacant during and just after the mating season (pers. obs.). Laboratory reared spiders of size 9, 10, and occasionally, 11 often molted to mature males. The emerged males probably die during or shortly after the mating season. Adult males were never found in the field after the mating season (July-September) in this study or in Coyle's (1971). Unfortunately, size classes 12, 13, and

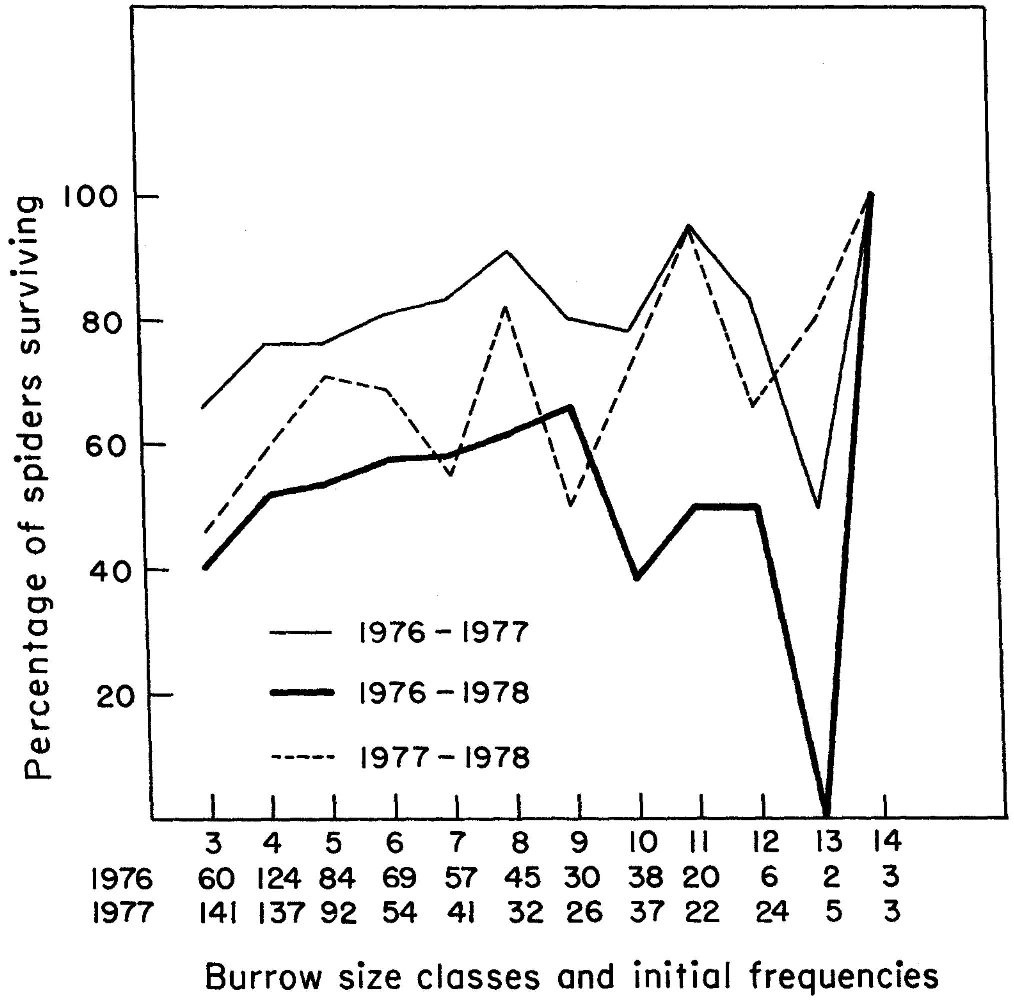

Figure 4.—Survivorship curves, based on burrow censuses, for spiders in initial size classes 3–14 for two one-year periods and one two-year period.

14 had too few members to suggest any trends, yet it should be noted that none of the size class 14 individuals died during this study.

Survivorship was lower for spiders in most size classes, especially size class 3, from July 1977 to August 1978 than from September 1976 to July 1977 (Fig. 4). In the two year interval, 1976–1978, over 50% of the spiders survived for all size classes except 3, 10 and 13. The curve for 1976–1978 resembles the 1976–1977 survivorship curve but is proportionally lower.

Several mortality agents (fungi, nematodes, and acrocerid and tachinid flies) of *A. riversi* were reared in the laboratory from egg sacs or spiders of the larger size classes (Vincent 1983, 1985). Unfortunately, I was unable to rear all the parasites and parasitoids to maturity for complete identification. In most cases the final size class of the dead spider (presumably killed by the action of the agent) was determined. Those mortality agents isolated in the laboratory and the pompilid *Priocnemis oregona* in the field are probably responsible for some of the mortality recorded in the study site. Pathogens or parasitoids were not isolated from spider sizes 3–8 (although one egg sac did contain some dead eggs contaminated with a fungus). This suggests that the more mature spiders are the usual victims of these mortality agents. It is not known at what stage in the spider's development it is first attacked by the agent (except for those parasitized by *P. oregona*).

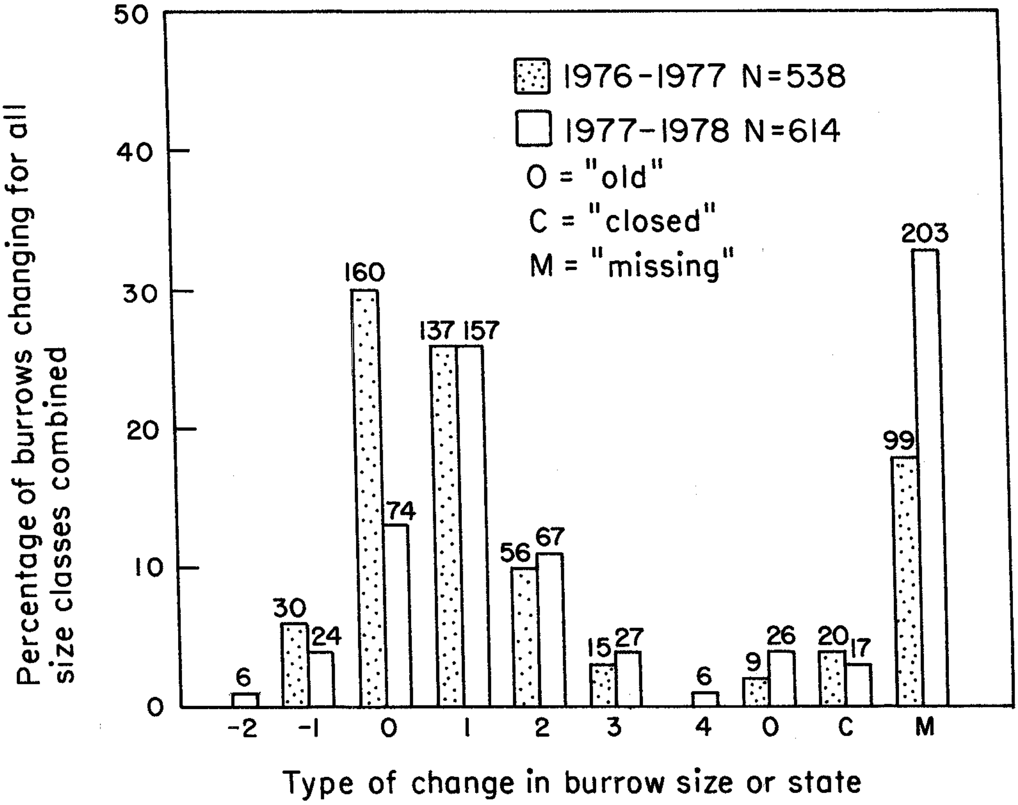

Figure 5.—Change in burrow size or state for all burrows present September 1976 and recensused July 1977 and all burrows present July 1977 and recensused August 1978.

For the present, I suspect desiccation, cannibalism, and starvation to be the most significant mortality factors for spiderlings. On several occasions spiderlings placed in non-moistened containers for transport to the laboratory from the field were found dead and shriveled a few hours later. Larger specimens of *A. riversi* kept under similar conditions did not desiccate. Coyle (1971) also noted that second instar spiderlings, the dispersal stage, desiccated quickly unless kept in high humidity. If desiccation is a factor, it most likely occurs during the dry summer months (see July 1977 and August 1978 demographics for burrows found in the previous spring); there was 1 cm precipitation from June through August both in 1977 and 1978. Cannibalism may be significant, especially in dense populations, since positive geotropism might influence spiderlings dispersing in search of burrow sites to enter occupied spider burrows. The proportionally large number of missing burrows in the smaller size classes during the April 1977 random sample and the May 1978 census suggests that starvation during the winter, when food is limited due to snow cover and cold temperatures, may be a significant mortality factor for spiderlings.

Longevity.—Mygalomorph spiders have been known to live a long time. Baerg (1963) kept certain theraphosids alive for at least 20 years in the laboratory and believed that one specimen lived 26 years (Baerg 1970). B. Y. Main (pers. comm.) estimates that a ctenized, *Anidiops villosus* (Rainbow), can live at least 23 years in the field. In estimating longevity of *A. riversi*, it is necessary to approximate several factors: date of oviposition and eclosion, date of emergence and burrow establishment, number of years to reach a size 14 (the largest size class), and the tenure of this size class. Since oviposition and eclosion occur in the summer and early fall respectively, and emergence in the following spring, the spiders in the size 3 burrows in September were about a year old. Based on extrapolations from the growth rates observed for all size classes from September 1976 to August 1978 (Table 3), the time it could take a size 3 burrow to become a size 14 varied considerably. Size classes 3 and 4 most frequently grew one size class in two years, size class five most frequently grew two size classes in two years, size class seven commonly grew three size classes in two years, and sizes classes 10 and 12 could grow two size classes in two years. Using these growth rates as an estimate, it would take some burrows 13 years to reach size 14. Other extrapolations, from Table 3, could reasonably be used to estimate minimum to maximum time to size class 14. Finally, in September of 1976 there were three size 14 spiders; on 22 September 1979, three years later, one was still alive. I estimate, therefore, that under similar environmental conditions and growth rates *A. riversi* can live in the field at least 16 years.

Most spiders (araneomorphs) live one to three years depending on the species (Bonnet 1935). Why do mygalomorphs live so long? Main (1976), referring to arid adapted trapdoor spiders, suggests it is advantageous for an adult female to be able to wait out several continuous years of unfavorable weather conditions that may disrupt the emergence of reproductively active males. In the fall, at Blodgett Forest, few females with eggs or brood were collected, yet during the spring many gravid females were collected. Lack of egg deposition could be due to insufficient acquisition of food during the summer for complete egg development by fall. Living several years would increase the chances of obtaining enough food. Unlike some araneomorphs (Turnbull 1964, Riechert 1976), *A. riversi* does not appear to change initial burrow locations to take advantage of potentially more productive areas.

In addition to biotic mechanisms, *A. riversi* may achieve a relatively long life because of its sheltered microhabitat. It has been suggested that the burrowing desert scorpion *Paruroctonus mesaensis* (Vaejovidae) achieved its long life (ca. five years) as one result of its stable and predictable subterranean microhabitat (Polis & Farley 1980). The burrows of *A. riversi* protect them from wind, to some extent rain and runoff, and some potential predators. Additionally, an influx of moisture from surrounding soil (Vogel 1978) and regulating the turret entrance opening (Vincent pers. obs.) may help prevent desiccation during the dry California summers.

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