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PHENOLOGY AND LIFE HISTORY OF THE DESERT SPIDER, *DIGUETIA MOJAVEA* (ARANEAE, DIGUETIDAE)

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ABSTRACT. The desert spider, *Diguetia mojavea* Gertsch 1958, is a numerical dominant in many California deserts. We report data collected over a three-year period (1984–86) on reproduction, life history, phenology, microhabitat, prey, and dispersion for *D. mojavea* in the Coachella Valley, California. This is one of few studies to calculate life history table parameters for a desert arachnid. The average female laid 1065 eggs, while the net reproductive rate (R_o) was 1.41; generation time (T) was calculated as 204.85 days. These spiders appear to fit a Type III survivorship curve. Density of *D. mojavea* was typical for a desert spider at 0.02 spiders/m^2. Finally, our findings complement the only other study on *D. mojavea* (Nuessly & Goeden 1984).

Spiders in the family Diguetidae Gertsch 1949 are primitive, six-eyed weavers contained in three genera, *Pertica* Simon 1903, *Segestrioides* Keyserling 1883 and *Diguetia* Simon 1895 (Platnick 1989). *Diguetia*, the dominant genus in this family, consists of spiders with elongate legs that weave characteristic funnel or net webs, or a combination thereof. Although they range widely from the southwestern United States to southern Mexico (Comstock 1948; Gertsch 1958; Lopez 1984) and parts of Argentina (Gerschman de Pikelin & Schiapelli 1962), few papers have focused on this family since its formal description by Gertsch (1949). Gerschman de Pikelin & Schiapelli (1962) studied the web characteristics of *D. catamarquensis* (Mello-Leitão 1941) in Argentina, Eberhard (1967) investigated prey capture and wrapping behavior in *D. albolineata* Simon 1898, and Bentzien (1973) described behavior and reproductive biology of *D. imperiosa* Gertsch & Mulaik 1940. *Diguetia canities* McCook 1895, the most widespread species (Cazier & Mortenson 1962), is best-studied due both to its relative abundance and its commercial importance in insecticide development (e.g., Krapcho et al. 1995; Hughes et al. 1997).

Diguetia mojavea Gertsch 1958 is distributed throughout southern California and adjacent areas in Nevada (Gertsch 1958), and it also appears to be one of the numerically dominant spider species in some California desert areas (Polis 1991). However, only one paper (Nuessly & Goeden 1984) focuses on the biology and ecology of this species, and a few others mention *D. mojavea* briefly (e.g., Polis & McCormick 1986; Polis 1991). Here, we examine *D. mojavea*'s phenology in more detail. We also report life history statistics used to calculate *D. mojavea*'s net reproductive rate and rate of potential increase both because of its significant role in various desert ecosystems and its potential impact as an important biological control agent (Nuessly & Goeden 1983).

METHODS

Relevant biology.—Several characteristics facilitate research on *D. mojavea*. First, populations are relatively dense (see Results). Second, the web of adults is large (mean length: 33.8 cm; mean width: 24.0 cm; see also Nuessly & Goeden 1984) and quite visible, especially in early morning or late afternoon at low sun angles. Third, the adult female web includes a retreat containing eggs, thus facilitating studies on reproductive biology. Fourth, prey and diet are easily quantified because *D. mojavea* incorporates most prey into its web (Gertsch 1958).

Study site.—Field studies were conducted within and adjacent to the Coachella Valley Reserve of southern California (Riverside County, California; 33°54′N, 166°37′ W). The Reserve encompasses about 780 km^2 and spans an elevational gradient from 320 m in the northwest to sea level in the southeast. Winters are mild; summers, hot and dry. Air temperature in July annually exceeds 40 °C and temperatures greater than 50 °C occur (Edney et al. 1974; Polis 1988). It is a low elevation rain shadow desert, with annual rainfall at the University of California's Deep Canyon Field Station averaging 116 mm, ranging from 34 mm in 1961 to 301 mm in 1976. Vegetation includes *Atriplex caescens* (saltbush), *Salsola australis* (Russian thistle), *Larrea tridentata* (creosote), *Tamarix* sp. (salt cedar), and annual plants and grasses. We surveyed web sites dispersed over an area of 7500 m^2 divided into 300 quardats, each 5 × 5 m. Quadrats were marked with flags and surveyed at least every three weeks from early June to September in 1984–86. Webs and egg sacs were also collected in December 1984–86 and 1997.

Egg sac analysis.—*Diguetia mojavea*'s egg morphology and egg sac construction are similar to *D. canities* (Cazier & Mortenson 1962). Each sac is constructed beneath the previous one in a shingle-like fashion, which is then incorporated into the tube retreat (Gertsch 1979). To examine seasonal patterns in egg-laying in August, September, and December 1984–86, we randomly chose 31 retreats to examine the number of egg sacs. All females were usually absent in our December survey (see Life history results); thus no new egg sacs could be laid, and these data are then used to estimate average number of egg sacs laid in a female's life. Egg sacs were dissected for egg counts. Stages within the sac were classified as either egg, embryo/deutovum, 1st instar, 2nd instar (based on cephalothorax length), or dead. Because maternal-guarding of the egg sacs seemed to play an important role in the life history of the adult females, we assumed each web contained only the resident female's eggs. Here as throughout the paper, means are reported with their standard deviations.

Spider web/microhabitat analysis.—For each spider in our quadrats, we recorded life stage (spiderling, adult) and sex of adults. Web characteristics were collected for the 137 webs in our plot in 1984. The volume of each web was calculated using height, width, and length. We measured retreat height and identified the plant on which webs were placed. Entire retreats and egg sacs were randomly collected in 1985–86 outside our quadrats. These were preserved in alcohol. For these spiders, we recorded adult-spider mass, the number of egg sacs and the egg stage (see above) for each web.

Prey analysis.—We examined diet by analyzing the prey from 111 retreats collected from 1984–86. Most prey are incorporated into the web, but some very large prey were discarded into the sheet or onto the ground. Prey items were easily separated from the web using a dilute bleach solution (Nuessly & Goeden 1984). A separate sub-sample (n = 26) of prey was taken from the sheet-web for analysis. Collected prey were identified to order and/or family.

Dispersion, phenology and life history.—The 300 quadrats in our survey area of 7500 m^2 were censused throughout the study to determine *D. mojavea*'s density, phenology and dispersion. These data were used to calculate survivorship curves and a Greig-Smith block size analysis in 1984 (Pielou 1977). This particular dispersion analysis determines if organism-spacing is aggregated, regular, or random. Fecundity variables (Pianka 1978) were also calculated. Parameters l_x (fraction of surviving spiders at age X) and m_x (number of offspring produced by an average spider at age X) were used to calculate net reproductive rate (R_o) and generation time (T). All formulae follow Pianka (1978).

RESULTS

Phenology.—The life cycle of *D. mojavea* encompasses approximately one year. Spiderlings emerge in late December through March. Females mature in May through June; the first egg sacs are produced in August through September (Figs. 1, 2), 2–3 months after the last molt. Approximately 85% of all egg sacs are laid during this two month period. Adult males first appeared in July. From 1984–86, adult females senesced and died from October to mid-December. In 1997, a few adult females were observed living in their webs as late as 20 December (7 out of 31). Males typically died one to two months before females (Fig. 2). We observed males in 14% of the 137 webs collected in July-September. The average mass of the adult females was 36.8 ± 23.6 mg, with a mean carapace length of 3.8 ± 0.8 mm. From our 1997 sample, the mean carapace length of 1st instar spiderlings was 0.66 ± 0.03 mm.

Egg sac analysis.—All egg cases appeared to be laid by late September. One to 13 total

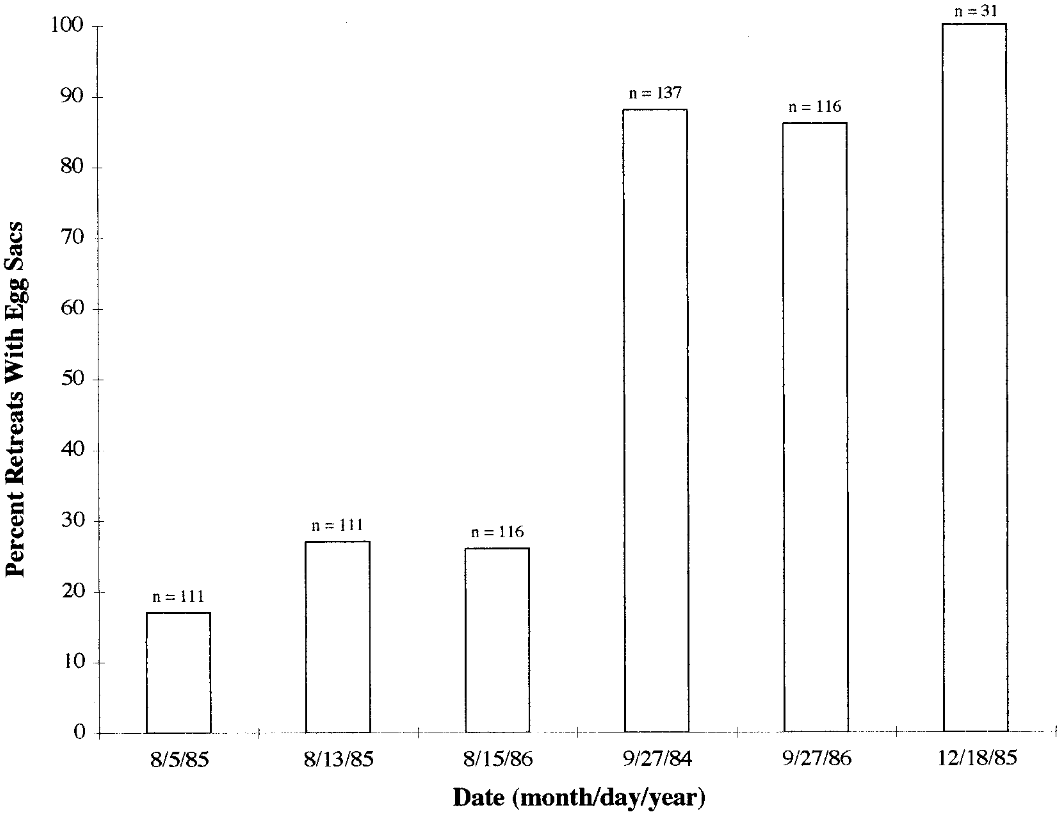

Figure 1.—Oviposition phenology. Seasonal changes in percentage of webs of *D. mojavea* found with egg sacs ($n = 96$).

egg cases were laid per female. All 31 retreats examined in our December collection contained egg sacs (Fig. 1); the number of egg sacs and the total number of eggs a female laid were significantly correlated (Fig. 3). Over the three-year period (1984–86), we collected 364 webs that contained 1083 intact egg cases. The average number of egg cases per female was 4.9 ± 2.7 (Fig. 4). The mean number of eggs per sac from 1984–86 was 217.4 ± 31.6, data taken from a subsample of 237 egg cases. Thus, the mean number of eggs laid per female was 1065.3 ± 381.2.

Egg sacs were laid over a period of days as evidenced by personal observation, presence of multiple egg sacs, and staggered emergence of spiderlings. We examined the stage of development for the dissected sub-set ($n = 237$) of the egg sacs we collected. Each case contained only individuals in the same developmental phase. However, developmental stage did differ among egg cases within a particular female's retreat. Of the 237 cases examined, 47% ($n = 111$) were classified as containing eggs; 19%, embryos (deutova); 17%, 1st instar; 4%, 2nd instar; and 13%, shriveled, dead eggs. The sequence of development followed the order in which the sacs were deposited: the uppermost egg sac located at the tip of the retreat always contained the most advanced stage, and sacs toward the retreat opening contained only eggs.

Web/microhabitat analysis.—The first typical webs we noted were built in late May by spiders with a body length of 3–4 mm. As the summer progressed, webs became larger and were placed in progressively higher vegetation. The mean size of a web in early summer (10 June) was 28.3 cm in length (range: 10–50 cm) by 21.1 cm across (range: 10–43 cm). By mid-summer, mean size increased to 33.8 cm (20–60 cm) by 24.0 cm (12–40 cm). There was a significant correlation between spider weight and web volume (Fig. 5) and

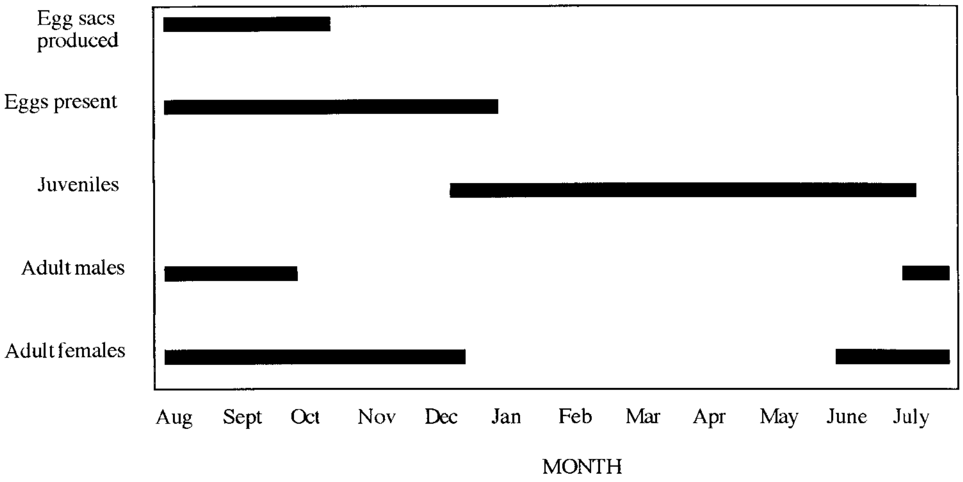

Figure 2.—Phenology. Bars show months in which each stage occurred. Data collected from 1984–1986.

between shrub height and spider weight (Fig. 6) (analyses conducted on July/August data).

Web location changed throughout the year with less desirable sites (i.e., dead bushes) supporting progressively fewer spiders. In early summer, 68.6% of the webs were built in perennial bushes (39.8% in *Atriplex* and 28.8% in *Salsola*), while the remaining 31.4% were placed in both living and dead annuals. *Larrea* and *Tamarix* were only rarely used as web-sites possibly due to their thin, exposed and flexible branches. Webs persisting into late summer remained only on larger *Atriplex* and *Salsola* as winds damaged and uprooted annual plants. Moreover, 43.8% of monitored webs were torn by wind and/or abandoned; unprotected web sites near the ground represented 72.1% of these cases.

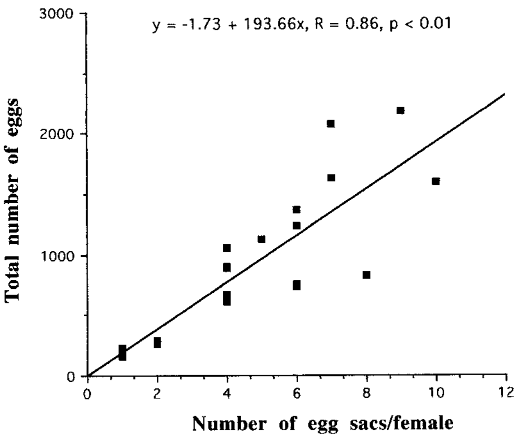

Figure 3.—Egg production. The number of eggs laid per female was significantly correlated with the total number of egg sacs ($y = -1.73 + 193.66x$, $R = 0.86$, $P < 0.01$), number of retreats examined = 31.

Prey analysis.—From May through October, spiders were observed feeding primarily in early morning or late afternoon, thus avoiding the mid-day heat. Prey capture was observed on several occasions. After prey were detected in the web, the resident would run to the prey and immediately (< 10 seconds) immobilize it with a bite. Silk, although used to secure prey to the web, was not used for immobilization (see also Eberhard 1967).

Prey remains were analyzed from 111 webs; a total of 6771 individual prey was identified to order and/or family (Table 1). On average, each web contained 61 ± 17.8 prey items; mean prey-size in retreats was 5.2 ± 0.9 mm. Homoptera (Cicadellids), small Hymenoptera, and Coleoptera comprised 88.1% of *D. mojavea*'s diet. A coleopteran egg predator (Cleridae, *Phyllobaenus discoideus*) was occasionally caught. Five other spider species comprised 3.4% of the diet and occurred in 30% of examined retreats. Cannibalism was recorded three times.

The sheet-web subsample (*n* = 26) yielded fewer (< 5 prey/sheet-web) but much larger prey (14.9 ± 6.0 mm; 131 prey analyzed). Only 3% of all prey items (mean = 1.9 ± 0.7)

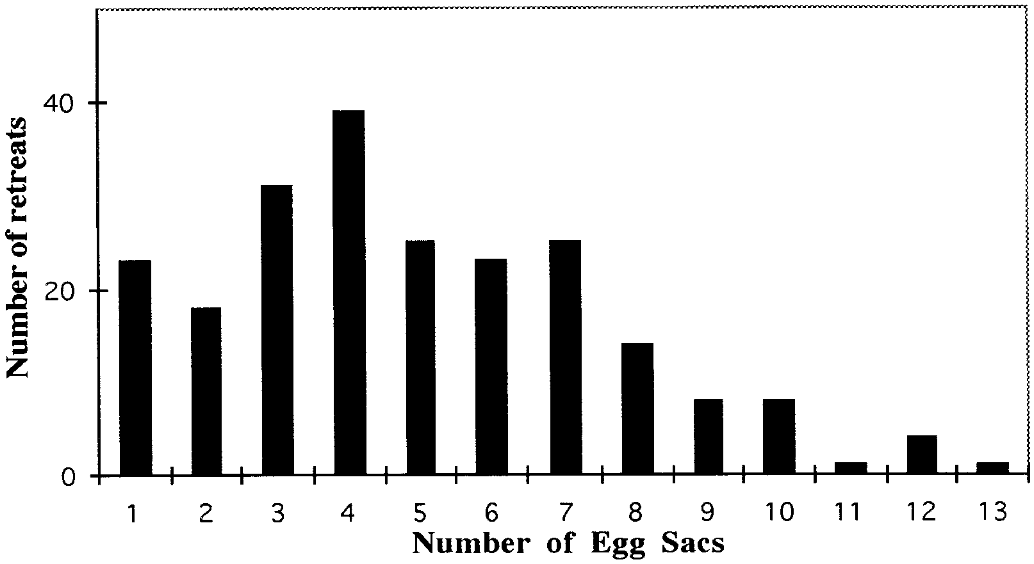

Figure 4.—Distribution of egg sacs in retreats. Egg sac number per retreat for data from 1984–1986 (total number of egg sacs examined = 364).

were dropped on the sheet-web by the spider. Although we did not measure biomass, large prey certainly represented more than 3% of total prey biomass. The largest prey items were a mantid (25 mm), mud dauber wasp (25 mm), robber fly (24 mm), and cicadid (24 mm). Grasshoppers were the most common larger prey in sheet-webs but constituted less than 1% of *D. mojavea*'s total diet.

Mortality and survivorship.—Several predators were observed in diguetid webs. Clerid beetle larvae (*P. discoideus*), reported egg predators (Cazier & Mortenson 1962), emerged in the lab from about one-seventh of the webs analyzed ($n = 137$). Salticids were observed eating both diguetid eggs and adults;

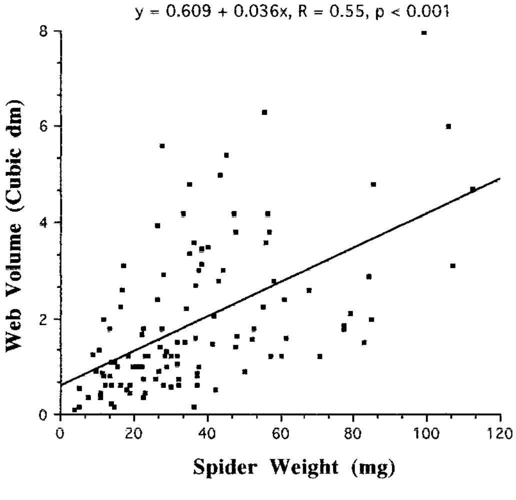

Figure 5.—Web volume as a function of spider mass. Spider weight was significantly correlated with web volume ($y = 0.609 + 0.036x$, $R = 0.55$, $P < 0.001$) for all three years combined (1984–1986).

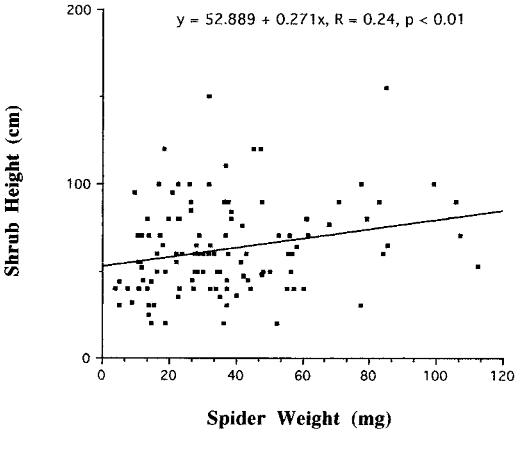

Figure 6.—Shrub height as a function of spider mass. Spider weight was significantly correlated with shrub height ($y = 52.889 + 0.271x$, $R = 0.24$, $P < 0.01$). Data are for all three years combined (1984–1986).

Table 1.—Prey of *Dignetia mojavea.* Italics indicate prey orders with families listed beneath when possible. Numbers in parentheses indicate total for the group.

Taxa	% of diet	% Occurrence among retreats
Arachnida	(3.4)	*30*
Diguetidae	1.0	
Mimetidae	0.8	
Oxypidae	0.2	
Salticidae	1.4	
Hemiptera		
(e.g., Pentatomidae)	(2.2)	*16.2*
Homoptera	(36.7)	
Cicadellidae	33.9	*80.2*
Cicadidae	0.1	
Isoptera	($<$0.01)	*0.05*
Orthoptera		
(e.g., Acrididae, Mantidae)	(0.5)	*4.5*
Coleoptera	(17.9)	*61.3*
Tenebrionidae	16.9	
Cleridae	0.01	
Diptera		
(e.g., Asilidae)	(3.4)	*23.4*
Hymenoptera	(33.5)	
Pompillidae	27.3	
Apidae	3.2	
Formicidae	2.9	
Sphecidae	0.1	*79.3*
Lepidoptera		
(e.g., Coleophoridae)	(2.2)	*14.4*

Habronattus tranquillus and *Metaphidippus manni* (G. & E. Peckham) appeared to be the most frequent predators of *D. mojavea*. Parasitism was not observed in this study.

Figure 7 shows average spider density through time summed over all quadrats in 1984. Adult density decreased in an almost linear fashion throughout the summer from July through September 1984, while egg production increased throughout each summer. If we assume that egg production in 1983 was similar in our plot to that in 1984, only 137 females in 7500 m^2 out of approximately 123,600 eggs survived to adulthood ($<$ 0.01%). This represents a Type III survivorship curve (Pianka 1978). Finally, adult density decreased from 0.02 spiders/m^2 (137 spiders/7500 m^2) in July to 0.003 spiders/m^2 (19 spiders/m^2) in September.

Dispersion.—A Greig-Smith block size analysis of dispersion (Fig. 8) indicated that these spiders were not randomly dispersed in our study plots. Significant aggregations appeared at block sizes of 1 and 8 m.

Life history.—We calculated life history statistics using the data on number of eggs laid per female and spiderling/adult emergence/survival. Table 2 summarizes fecundity variables (Pianka 1978). The empirical net reproductive rate, R_o, (Pianka 1978) was 1.41, which was easily calculated since all spiders remaining at the end of the season were female. Generation time (T) was calculated as 204.85 days. The average number of eggs laid per female (1065.3) was applied to all adult females with egg cases, making m_x (the number of offspring produced by an average organism at age X) equal to 1.0 (or 100%) for August and September age values (i.e., egg cases were present in August through October; Fig. 2). For the July age class, m_x was 0.0 because no egg cases were observed before

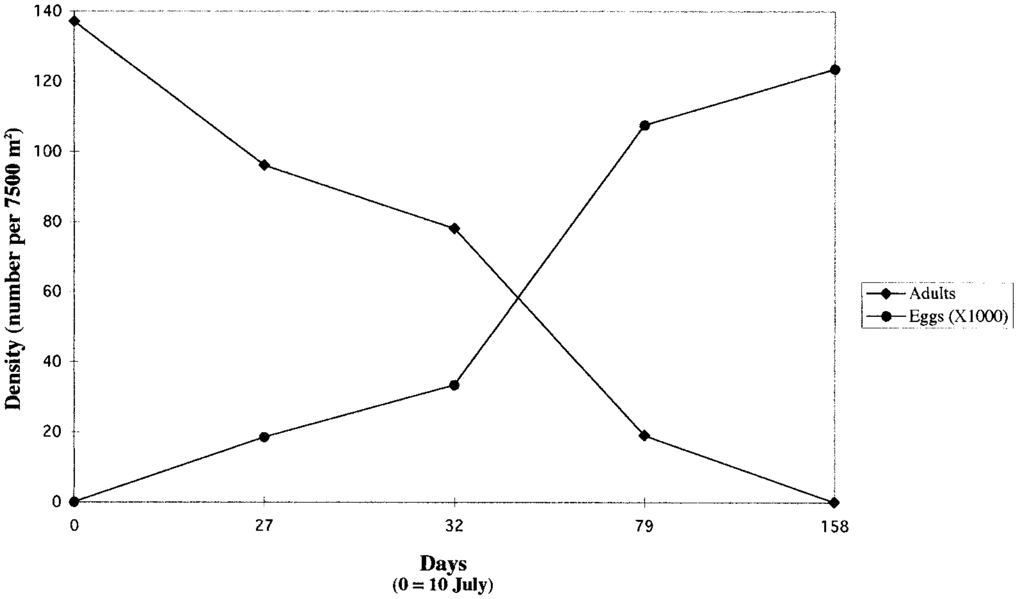

Figure 7.—Survivorship. Spider density decreases as time of season increases while egg number (×1000) increases throughout the season. Data are from 1984.

August. The maximum rate of natural increase, r_{max} (ln R_o/T) was calculated as 1.68 × 10^{-3}/d.

DISCUSSION

There are a number of unique morphological and ecological characteristics exhibited by *D. mojavea*.

Phenology.—Recall that we observed hatching of spiderlings in the field from December-March, adult females from June-December, adult males from July-October, and egg-laying from August-October. The univoltine and semelparous qualities of *D. mojavea* are typical of other diguetids (e.g., Bentzien 1973) and other spiders, in general (Foelix 1996). Moreover, a similar 1-year, 1-egg sac pattern is found in many desert arthropods, which may be due to the costliness of egg production and longevity in desert ecosystems (Polis 1991).

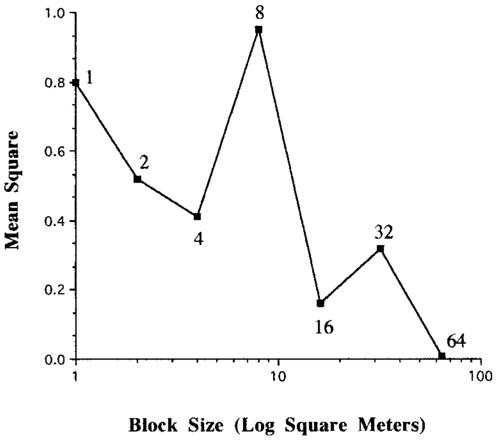

Figure 8.—Dispersion analysis. Greig-Smith block size analysis shows statistically significant aggregations at 1 and 8 m blocks. Data are from 1984.

Reproduction and life history.—Our observations indicated that egg production in *D. mojavea* is slightly lower than that reported by Nuessly & Goeden (1984) (an average of 6.4 egg sacs/nest with a mean of 176 eggs/sac for a total of 1126 eggs/web). *Diguetia mojavea*'s egg production fits well within the range of eggs produced by other spiders (Foelix 1996).

Staggered emergence is seen in spiders that have multiple egg sacs. This tactic may provide insurance against synchronous emergence during unfavorable conditions in harsh environments such as the desert. Thus, *D. mojavea* lessens the risk of failure through variable hatching times. Such a strategy is also seen in certain annual weed species and var-

Table 2.—Life history parameters calculated from the data collected throughout the study: l_x = fraction of spiders surviving at age X; m_x = the number of offspring produced by an average spider at age X; $l_x m_x$ = fecundity schedule; R_o = net reproductive rate; T = generation time (days). Formulae are based on Pianka (1978).

Age (X) in days	l_x	m_x	$l_x m_x$	$Xl_x m_x$
101	1.0	0.0	0.0	0.0
138	0.7	1.0	0.7	96.6
143	0.57	1.0	0.57	81.51
191	0.14	1.0	0.14	26.74
Total			R_o = 1.41	T = 204.85

ious other opportunistic species in the desert environment (Polis 1991). Staggered emergence is observed in most spiders that have multiple egg sacs (e.g., Bristowe 1958; Jackson 1978); it is probably an adaptation to high parasitoid pressure and/or harsh abiotic conditions.

The net reproductive rate indicates that this population could potentially increase 1.41 times per generation. The maximum rate of increase is one of the lowest ever reported (e.g., Pianka 1970) even when compared to other arachnids (e.g., scorpions from Polis & Farley 1980). This finding may reflect the high rate of egg mortality and low survivorship of females to first age of reproduction.

Mortality.—Our sample produced a Type III survivorship curve. Many desert inhabitants have high mortality rates in the early stages of their life history (Polis & Yamashita 1991), which may be caused by a variety of desert stresses. We observed a number of predators preying on diguetid adults and eggs. Nuessly & Goeden (1984), on the other hand, observed molting only as a cause of mortality in the field.

Prey analysis.—Spiders, on the whole, are usually characterized as generalist predators (Foelix 1996). Our results reinforce this generalization. *Diguetia mojavea* consumed prey from 10 orders. Homoptera, Hymenoptera, and Coleoptera made up most (more than 88.7%) of *D. mojavea*'s diet. This finding contrasts Nuessly & Goeden's (1984) report, who noted that the introduced biological control agent, a coleophorid moth, accounted for nearly 70% of *D. mojavea*'s diet in Indio, California; less than 3% of the diet in our study consisted of this moth. This discrepancy is probably to due to the fact that Indio has had several introductions of this moth for control of *Salsola*. Our site remains relatively undisturbed from this introduction.

Our analysis of prey contents in their sheetwebs is a first for diguetids. These prey had more biomass than those prey incorporated into the retreat but constituted a numerically minute (3%) amount of the total diet. This may be due to the inherent difficulty of capturing and/or handling larger prey.

Previous findings.—Nuessly & Goeden's (1984) paper is the only other study to examine the natural history of *D. mojavea*. They noted the following characteristics: a one-year life cycle; a diet consisting largely of coleophorids and cicadellids; a significant positive correlation between number of prey and egg number; and observed mortality due only to molting with no direct evidence of predation. They did not calculate life history parameters of reproduction and survivorship. Several differences existed between our study and that of Nuessly & Goeden's (1984). Their study was conducted at Indio, California for six months, a recently cultivated area populated by an invasive weed community. Our study was much longer (3.5 years) and was conducted on the floor of the Coachella Valley, which is a natural, undisturbed area.

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