

Predation versus resource limitation in survival of adult burrowing wolf spiders (Araneae: Lycosidae)

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Summary. The influences of food supply and density on adult survival were examined in the burrowing wolf spider *Geolycosa rafaellana* (Lycosidae), using manipulations of spider populations on eight 400 sq m experimental plots. A total of 110 adult spiders were captured, weighed, marked, and returned to their burrows during April–May 1983. Treatments of (1) food supplementation, (2) density reduction, (3) food supplementation combined with density reduction, and (4) no manipulation (control) were applied to the eight populations, and adult survival and reproduction were monitored during May–October 1983. Survival rates were higher for nonreproducing adult female populations with reduced density, and lower for nonreproducing females in populations with food supplementation. A pompilid wasp, *Paracyphononyx funereus*, was documented as a parasitoid of *G. rafaellana*, producing 50%–65% mortality in adult females during winter, and 4–5% mortality in adult females during summer. The observed survival responses were correlated with variations in predation, while parasitism did not appear to be strongly density-dependent.

Investigations of spider population regulation have traditionally addressed documentation of intra- and interspecific competition through identification of limiting resources. Limitation by web site availability is known for some species (Riechert 1974; Schaefer 1978), but efforts to demonstrate food limitation have produced conflicting conclusions. Greenstone (1978) found that food was not a limiting resource for *Pardosa* (Lycosidae) and proposed that numerical responses (increased survival or reproduction in response to increased prey density) are improbable in spiders because physiological adaptations avoid food limitation. In contrast, Van Wingerden (1978) found egg production to be correlated with prey abundance in *Eriogone* (Linyphiidae). Wise (1975) demonstrated increased survival and fecundity in response to food supplementation in *Linyphia* (Linyphiidae) and increased egg production in response to food supplementation in two orb-weaving spiders (Wise 1979). Evidence of food limitation in *Lycosa* (Lycosidae) is presented by Sasaba and Kiritani (1974) and Kobayashi (1975).

In the present study, a factorial design was employed in a manipulative field experiment to assess food and/or density limitation on adult survival in a lycosid spider. In addition to monitoring of mortality patterns as a response

variable, mortality factors were also identified. This aspect of the results (largely absent from experimental field studies) served to enlarge the realm of explanatory mechanisms beyond the paradigm of competitive limitation.

Geolycosa rafaellana (Chamberlin) is a burrow dwelling lycosid which occurs in desert and desert-grassland areas throughout the southwestern United States (Wallace 1942). Adult spiders construct a tubular burrow that extends straight down 20–30 cm, terminating in a slightly enlarged side chamber at the bottom. Feeding activity is largely nocturnal during May–September, and consists of motionless surveillance at the burrow entrance and capture of prey moving near the burrow. With the exception of male mating excursions and occasional foraging within 2–3 cm of the burrow entrance by juveniles (personal observation), the species is extremely sedentary. Adult populations do not display burrow re-location; the burrow established by each subadult spider is occupied through adulthood until death. Physiological ecology, activity patterns, and demographic patterns for other species of *Geolycosa* are known from work by Humphreys (1974, 1975a, 1975b, 1978), McQueen (1978, 1979, 1980, 1983) and McQueen and Culik (1981). *G. rafaellana* features a three year life cycle, similar to that described by McQueen (1978) for *G. domifex*. Adults mate during early spring (February–March) and females produce egg sacs during May and June. Juveniles disperse from the maternal burrow during July–August, overwinter in the soil, and emerge to construct burrows in the spring. The cohort reaches maturity in the spring when 32–34 months old, and males die during the following summer. Females mate with the males of their own cohort, and a variable number survive an additional year to mate with males of the following cohort. Thus males display a three year lifespan, while females may live four years. The potential for doubling individual reproductive output through enhanced adult female survival is an integral feature of this study.

Methods

This study was conducted at the New Mexico State University College Ranch, approximately 40 km NNE of Las Cruces, New Mexico, USA. The site is in the northern Chihuahuan Desert and features sandy to sandy loam soils with sparse vegetative cover of scattered shrubs and perennial and annual herbs and grasses.

Eight 20 m × 20 m (400 m²) experimental plots were established in March 1983, and adult spider burrows on each

plot were censused, mapped, and marked with aluminum tags. Census and mapping were facilitated by division of each plot into 25 16-m² segments (using survey string), allowing systematic searches of each plot (by segment), repeated on two occasions prior to the beginning of manipulations. During March–April, adult spiders were captured using an adhesive bait technique (Conley 1985), weighed, marked with fluorescent paint applied to legs, and returned to burrows. Marking was used to document permanence of burrow occupation by adult female spiders, allowing identification of stable experimental populations, and weights were used in determination of adult status. Adult female spiders exhibited decreasing receptivity to the capture technique at the onset of egg sac production, resulting in failure to capture some individuals. Unmarked individuals were included in the feeding regime on plots with food supplementation, and survival and reproductive data were collected for both marked and unmarked individuals.

The following treatments were allocated at random to the eight plots, with two plots receiving each treatment: (1) removal of approximately 50% of adult female spiders present, (2) weekly food supplementation consisting of one mealworm (*Tenebrio* sp.) per adult spider, (3) density reduction as in # 1 and food supplementation (# 2), and (4) control-no density or food manipulations. Removals occurred concurrent with marking; food supplementation began in May and continued through September. Burrows were examined monthly for survival and activity and reproductive status of occupants, and all burrows were excavated in late October to provide additional data on reproduction (remains of egg sacs), fate of spider (presence of spider or its remains, and cocoons of parasitoid), and food habits (arthropod remains). Four additional plots were established concurrently for use in a companion experiment and spider populations on these plots were censused and monitored without disturbance. (Data from these plots are included in descriptions of mortality patterns.)

Reproductive output was not considered as a response variable in this study, although probability of survival of adult females to a second summer is an integral feature in calculating reproductive values. Accurate measurement of fecundity would require capture of females with egg sacs and lab rearing until young appear, which would eliminate a valid assessment of survival of natural populations in the post-reproductive season. Because mating had already occurred when experimental treatments began, the proportion of females reproducing can not be interpreted as a treatment effect.

Treating plots as experimental units, the survival rate of the adult female population on each plot was estimated from numbers of weighed, marked females surviving at each observation period. Survival of male spiders was excluded from analysis of treatment effects, since males die (due to predation or natural death) shortly after the mating season, irrespective of external factors. Treatment responses of reproductive females and nonreproductive females were considered separately, based upon the survival implications of the energetic costs of reproduction. Female spiders weighing less than 400 mg were excluded from the analysis, based on literature evidence for a similar species (McQueen 1978) and reproductive data from this study, which indicate this to be a minimum weight for reproduction. Logarithmic transformations of observed numbers were applied in regressions using an exponential decay model ($N_t = N_0 e^{-rt}$).

Capture difficulties noted earlier resulted in unequal replication of treatments for marked individuals; for each pair of replicate plots, the slopes of individual regression lines were compared using an F-test, and replicates not differing significantly ($P > 0.05$) were pooled (Snedecor and Cochran 1967). The same technique was then applied in comparing treatment populations to controls. A factorial analysis of variance was also applied to survival data for adult females, with marked and unmarked individuals pooled.

Results

Food and density

Survival rates (r) for marked reproducing females in the three treatment populations were not significantly different ($P > 0.05$) from that of the control population (Fig. 1). The estimated survival rate for marked non-reproducing females in one population with reduced density and normal food supply ($r = -0.046$) was significantly higher ($0.01 < P < 0.05$) than that for non-reproducing females in the control populations.

With marked and unmarked individuals combined in a factorial analysis of variance (with time entered as a covariate), food and density again were not significant factors in determining survival among reproducing adult females. For non-reproducing females, both food and density were significant ($P < 0.05$) factors in determining survival, with no significant interaction effect. Treatment means indicate higher percent survival with reduced density and lower percent survival with food supplementation.

Parasitism

Five wasps reared from parasitized female spiders were identified as *Paracyphononyx funereus* Lep. (Pompilidae).

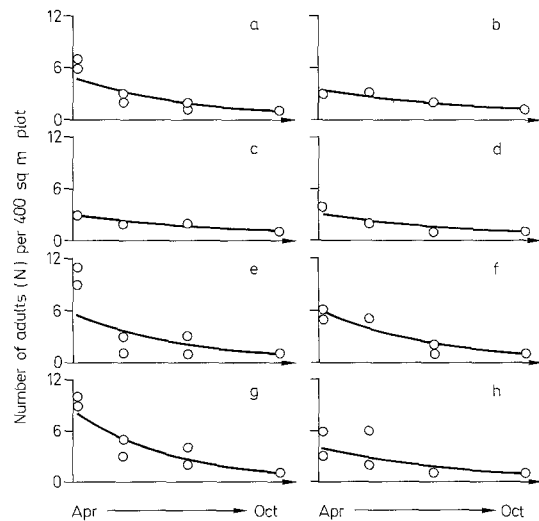


Fig. 1A–H. Survival of marked adult female spiders in experimental 400 m² plots; A, C, E, and G – non-reproducing females; B, D, F and H – reproducing females; A, B – populations with density reduction and food supplementation, C, D – populations with density reduction, E, F – populations with food supplementation, G, H – populations with no manipulation (controls). Regression lines are from an exponential decay model ($N_t = N_0 e^{-rt}$). Data for categories A, E, F, G and H are from replicate plots; treatments were not replicated among marked females in categories B, C and D