FORAGING ACTIVITY AND BURROW DISTRIBUTION IN THE SYDNEY BROWN TRAPDOOR SPIDER (*MISGOLAS RAPAX* KARSCH: IDIOPIDAE)

Richard A. Bradley: Ohio State University, 1465 Mt. Vernon Ave., Marion, Ohio 43302 USA

ABSTRACT. Burrow-associated behavior of *Misgolas rapax* was observed in the field and laboratory. Spider density was estimated on 16 replicate plots at one study site in Brisbane Water National Park, NSW, Australia. These estimates were compared to habitat features including vegetation, topographic slope and soil penetrance. Spider burrow density varied significantly across the study plots and was significantly aggregated. There were no detectable patterns of relationship between habitat features and variation in *M. rapax* density. *Misgolas rapax* density and activity patterns were not related to natural variation in spatial and temporal patterns of prey-abundance. Field and laboratory experiments were conducted to determine the influence of proximate feeding history on activity in adult females. Foraging activity decreased after food supplementation in the field and was lower among the high-food treatment females in the laboratory. Despite the fact that *M. rapax* behavior is influenced by feeding history, these spiders are apparently unable to adjust their behavior to the unpredictable fluctuations in prey availability.

The Sydney brown trapdoor spider (*Misgolas rapax* Karsch 1878) is abundant in a variety of dry sclerophyll woodland habitats in SE coastal New South Wales, Australia. It builds a burrow lacking a trapdoor, but the entrance is occasionally sealed with silk and covered with leaves. Prey are captured from ambush at the burrow entrance, and adults rarely wander more than a few centimeters from the burrow. The sole exception to this pattern is the mate-searching behavior of males. One striking aspect of the biology of *M. rapax* is that an occupied burrow is either open or closed (sealed with silk) for long periods of time (weeks to months). Individuals of *Misgolas rapax* can be found at the entrance to their burrows waiting for prey in any month of the year. This pattern contrasts with other trapdoor spiders which aestivate for long periods during the summer months (Buchli 1969; Marples & Marples 1972) or dry periods (Main 1982). The current study was initiated to determine if proximate environmental factors, or the abundance of prey, might influence the foraging activity patterns of this species. Another pattern in this species is the tendency for many burrows to be located in some areas and few in adjacent, apparently similar, areas. This work on *M. rapax* was conducted

at the same time on the same study plots as similar work on the common orb-weaving spider *Argiope keyserlingi* Karsch 1878. In that species, density was related to features of vegetation that provided favored web sites (Bradley 1993). A second goal of the study was to examine the burrow density and dispersion patterns of *M. rapax* and their relationship to features of the habitat.

METHODS

Study site.—The study area was located in Brisbane Water National Park (33°33′S, 151°18′E) at the SE corner of the town of Pearl Beach, New South Wales, Australia. A set of sixteen 0.023 ha plots (15m × 15 m) was marked with wood corner posts. The plots were established on one hillside in a patch of dry sclerophyll woodland dominated by *Casuarina torulosa* (70% by frequency) such that no two plots were closer to each other than 5 m. Consult Bradley (1993) for a detailed description of the study plots and general study site. Other large burrowing spiders known from the study area included *Atrax robustus* Cambridge 1877, *Geolycosa godeffroyi* (L. Koch) 1865, *Hadronyche* sp.?, *Lycosa furcillata* L. Koch 1867, *Lycosa pictiventris* L.

Koch 1877 and *Misgolas gracilis* (Rainbow & Pulleine 1918).

Environmental measurement.—Weather records (rainfall, temperature) were obtained from the Crommelin Biological Research Station, a station within 500 m of the study area. Soil temperature (surface, 15 cm and 30 cm), air temperature, and relative humidity were continuously recorded with a Weathertronics thermograph and hygrothermograph located in a ventilated wooden box on the study area. Temperature and humidity were measured at the burrow entrance for each spider activity observation using a Novasina MIK-2000 portable hygrothermograph (Novasina AG, Zurich). Soil penetrance was measured with a Soiltest CL-700 penetrometer; 100 measurements were made on each plot using a stratified random sampling design. This device provides an indication of surface resistance, which has been implicated as an important factor in the choice of burrowing site in studies of other arachnids (Lamoral 1978; Bradley 1986; Polis & McCormick 1986). Average topographic slope was estimated for each plot by estimating total elevation change from highest to lowest point on the plot. Twelve vegetation variables (Bradley 1993) were subjected to principal components analysis. The principal component scores for each plot along the first two axes were compared to measures of *M. rapax* density using Pearson product-moment correlation. The dispersion pattern of burrows was analyzed using the variance/mean ratio method (Southwood 1966). Significance of this ratio was assessed by Kershaw's method of calculating *t* (Kershaw 1973).

Burrow characteristics.—Burrows of 48 adult *M. rapax* were excavated (a large hole was dug beside the burrow, which was then approached from the side); spiders were collected from 34 of these burrows and the midden of rejected prey remains (rejectamenta) was collected from 32 burrows. All rejectamenta were identified and a minimum number of prey of each taxon was estimated from the parts. Burrow depth, diameter at entrance (just below flared opening at point where burrow becomes cylindrical), orientation of opening, depth of protective silk-closure, and depth of midden were measured. Spider fang length (right), carapace length and the length of tibia I (right) were measured to 0.1 mm.

Spider activity measurement.—Burrow entrances were marked with numbered wood tongue depressors placed 30 cm S of the entrance ($n = 429$). Regular (approximately biweekly, on the same nights as prey samples) observations of marked burrows were made to determine if they were open and whether the spider was near the entrance. At each visit to a marked burrow, the temperature and relative humidity were also measured. Spider population density was estimated during December 1985 by counting the number of occupied burrows on each plot.

Prey abundance measurement.—Two measures of prey abundance were made. Samples of leaf-litter were collected adjacent to the study plots by removing all litter down to bare soil from a 0.25 m^2 area. Potential prey organisms were extracted using a modified Tullgren funnel (Southwood 1966). Two rows of five pitfall traps were placed on each plot; pits were separated by 2 m, and rows were 3 m from edge of plot. Pits 20 cm deep were constructed of 5 mm thick polyvinyl chloride tubing with an inside diameter of 11 cm buried flush with the soil surface. A removable sleeve was used within pits fitted on the bottom with 0.5 mm nylon mesh for drainage. Pits were covered when not in use but were left dry and open during sampling. Samples were collected over 24-hour periods on 18 dates between August 1994–February 1996. Potential prey captured from litter or pitfall samples were identified (usually to family) and measured to nearest 1 mm (body length). Dry-weight biomass was estimated using regression equations appropriate for each taxon (Rogers et al. 1976, 1977). In cases where no appropriate regression equation was available, one was calculated from specimens captured in the study area. Potential-prey samples (litters, pits) were compared to temporal patterns of *M. rapax* activity using Pearson product-moment correlation analysis of prey variables against the proportion of *M. rapax* burrows that were open with an active spider near the entrance. Prey samples were also compared to *M. rapax* density spatially (across plots) using ANOVA (repeated-measures design).

Laboratory feeding experiment.—Twenty-four adult female *M. rapax* were installed in individual 30 cm (tall) × 30 cm (deep) × 7 cm (wide) clear acrylic plastic ("Plexiglas") containers. Each container was first filled to

within 5 cm of the top with natural soil from near the study area. The spiders readily dug burrows in the containers and lined them with silk. The soil was kept damp with regular misting of distilled water. All spiders were housed in a room illuminated on a 12:12 cycle and maintained between 21–29 °C. Spiders were randomly divided into two groups. One group (high-food) was fed either one adult cricket (*Gryllus* sp.), one ultimate-instar meal-worm larva (*Tenebrio molitor* Linnaeus) or one adult mealworm beetle every other day. All prey items were weighed to the nearest 0.1 mg. The second group (low-food) was fed a similar meal once per 14 days. Spiders were only fed if they were in the "foraging position" within 3 cm of the top of the burrow entrance. The food item was presented to the spider by gently rubbing the silk near the entrance to the burrow until the spider grasped the item. If a prey item was not eaten, it was removed the following day. Each spider was weighed at the beginning (27 October 1984) and end of the experimental period (2 September 1985). For the test of differences in activity (proportion of nights in foraging position), the proportions were subjected to the arcsin transformation before analysis.

Field food-supplementation experiment.—Seventy-three active (in foraging position) adult female *M. rapax* were located and their burrows marked. Spiders were randomly divided into two groups. Spiders in one group (food-supplementation, $n = 30$) were fed one seventh (ultimate) instar mealworm larva on four successive nights (13–16 February 1986). The mealworm was presented to the spider by gently rubbing the silk near the entrance to the burrow until the spider grasped the mealworm. Spiders in the second group (unmanipulated, $n = 43$) were checked for activity by rubbing the silk, but they were not fed. No attempt was made to restrict natural capture of prey. All spiders were checked subsequently on 20 February and 10 March 1986; the spider was scored for activity and for whether the burrow entrance was open or closed (with silk).

RESULTS

Burrow characteristics.—Burrows of *M. rapax* were found in the loosely consolidated sandy soils across the entire study area. Burrows were lined with silk that was attached to the *Casuarina*-needle litter at the entrance. There were few attached radially-arranged leaf or twig lines, which are common features of other trapdoor spider (*Aganippe* O. Pickard-Cambridge 1877 and *Idiosoma* Ausserer 1871) burrows found in areas with a substantial leaf litter (Main 1984). Burrows were relatively vertical silk-lined tubes with a mean depth of 33.6 cm (SD = 8.1, $n = 47$) and mean entrance diameter of 22.3 mm (SD = 2.6, $n = 48$). Only 10% of the burrows contained a defensive-sock closure (mean depth of closure 16.0 cm; SD = 3.1; $n = 5$). Main (1984) also mentions the inconsistency of defensive-sock closures in *M. rapax* burrows. Most of the spiders located in excavated burrows were found at the bottom; some were found just below the silk closure, holding it closed with their chelicerae. The mean burrow depth was correlated with mean entrance diameter ($r = +0.26$, $P < 0.05$). Burrow diameter was correlated with spider carapace length ($r = +0.50$, $P < 0.01$) and fang length ($r = +0.49$, $P < 0.01$). The burrow opening of most *M. rapax* burrows was tilted at an angle. There was no significant bias to the orientation of the openings with respect to either slope or compass direction. Many burrows contained a midden of uneaten prey remains near the bottom of the burrow (mean depth 19.8 mm; SD = 10.5; $n = 26$).

Density and habitat relationships.—*Misgolas rapax* density varied by a factor of 6.4 across the study plots. The mean density estimate based on occupied burrows in December 1995 for all 16 plots combined was 391/ha ($n = 16$, SD = 236). Vegetation, elevation, and slope characteristics varied significantly across the plots (Bradley 1993) but there were no correlations with *M. rapax* density patterns. There was significant variation in soil penetrance across plots (ANOVA; $F = 12.9$; $df = 15, 1584$; $P \ll 0.001$), but this feature was not correlated with *M. rapax* density ($r = -0.35$, ns). The mean distance between burrows was 5.4 m (SD = 9.0). The dispersion of *M. rapax* burrows was significantly clumped with a variance/mean ratio of random point-to-burrow distances of 14.8 ($t = 13.9$, $P < 0.01$). This may reflect the tendency for young spiders to disperse relatively short distances from the maternal burrow before constructing their own burrows.
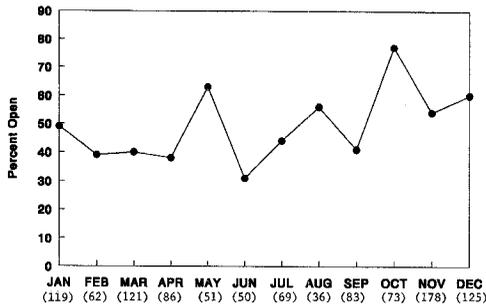
Activity patterns in field.—to assess "ac-

Figure 1.–Annual activity patterns of *Misgolas rapax*. The values in the figure represent the percentage of marked burrows which were open (active) and known to contain a live spider. The sample size of burrows checked is included in parentheses below the month.
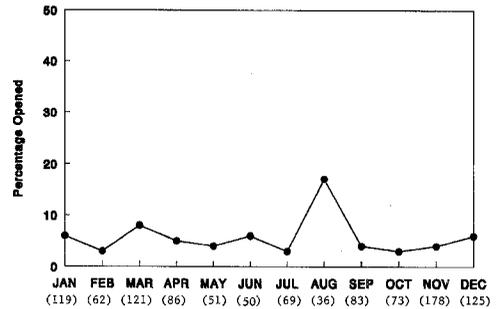

Figure 2.–The proportion of *Misgolas rapax* burrows that were discovered newly opened during the month indicated. The sample size of burrows checked is included in parentheses below the month.

tive" spiders, I analyzed observations of marked burrows. If a marked burrow was discovered closed and was never observed open again during the study, it was assumed that the spider had died or abandoned the burrow, and it was removed from the sample. Of the 429 marked burrows, activity data were scored for 1053 observations from 253 burrows known to contain a living *M. rapax* individual. These observations were made between September 1984–February 1986. The pattern of annual activity as indicated by the proportion of open burrows that were known to contain a living *M. rapax* is not strongly seasonal (Fig. 1). Similarly there is no obvious seasonal pattern to the proportion of previously-closed burrows which were opened during a particular month (Fig. 2). Burrows tended to remain open for long periods ($\bar{x}$ = 83 days, SD = 65, range 1–397 days). After a spider sealed the entrance to its burrow with silk, it typically remained closed for an extended interval ($\bar{x}$ = 76, SD = 60, range 6–332 days). On any given visit a burrow had a probability of 49.6% of being found open. Active *M. rapax* are usually visible near the entrance to the burrow (within three cm of the opening). The number of spiders in this foraging position was assessed during 722 observations at open burrows. Significantly more spiders were observed in the entrance of open burrows at night (18%) than during the day (7%) (t = 2.3; P < 0.05). There were no significant correlations between surface temperature, soil temperature or surface humidity and the tendency for a burrow to be open, or

for the spider to be in the active foraging position.

Relationship to potential-prey phenology.—Prey remains analyzed from the middens in excavated *M. rapax* burrows reveal that this spider eats substantial numbers of the large and aggressive bulldog ant *Myrmecia gulosa*. Unfortunately, the remains in middens undoubtedly contain a biased sample of prey; large and hard-bodied prey are probably overrepresented (Table 1).

A total of 2715 potential prey items was captured in the pitfall samples (this total excludes species known to be rejected by *M. rapax* in the laboratory). Prey availability (num-

Table 1.—Identified prey remains found in *Misgolas rapax* burrows (n = 287 prey; n = 32 middens).

Prey category	Percentage of burrows	Percentage of all prey
Myrmecia (Formicidae)	78	46
Carabidae	50	18
Scarabaeidae	41	5
Formicidae (others)	34	5
Coleoptera	28	4
Curculionidae	19	2
Hemiptera	13	2
Blattodea	13	1
Camponotus (Formicidae)	9	2
Cerambycidae	9	<1
Hymenoptera (others)	9	<1
Scorpionida	3	1
others	n/a	12

Table 2.—Results of the laboratory feeding experiment. [1]The sample size reflects differences in number of spiders surviving at the time of measurement. [2]The proportion of nights when a spider was seen in the "feeding position" within 3 cm of the top of the burrow.

Variable	High-food			Low-food			Significance	
	$\bar{x}$	SD	n^1	$\bar{x}$	SD	n^1	t	P
Number of meals	14	(9.1)	11	8	(2.9)	12	2.09	ns
Initial spider mass	2.38	(0.77)	12	2.47	(0.74)	12	−0.29	ns
Total food mass (g)	2.60	(1.44)	11	1.22	(0.43)	12	3.05	<0.05
Final spider mass (g)	2.83	(0.72)	11	2.36	(0.38)	12	−2.02	<0.05
Change in mass (g)	0.56	(0.73)	11	−0.11	(0.56)	12	−2.51	<0.05
Prop. nights active[2]	0.15	(0.13)	11	0.27	(0.16)	12	−2.13	<0.05

bers trapped) appears to vary significantly through the season as assessed by pitfall-trap samples (ANOVA $F = 2.17$; $df = 15, 272$; $P < 0.01$). Numbers and biomass of potential-prey both peak during spring or early summer (late September through December). Results from the litter samples appear less seasonal (ANOVA ns). Using proportion of spiders active (open burrow with spider near entrance) as an index of *M. rapax* temporal foraging phenology, there was a weak correlation with total potential-prey numbers captured in the pitfall-trap samples ($r = +0.57$; $P < 0.05$); this correlation disappears when the sample is restricted to the larger potential prey that comprise most of the diet of *M. rapax* ($r = +0.38$; ns). Similarly, there is no seasonal correlation with potential-prey biomass ($r = +0.42$; ns). There were no signficant correlations between *M. rapax* foraging phenology and potential prey in the litter samples.

Spatially, potential-prey abundance varied signficantly across the study plots for numbers ($F = 2.17$; $df = 15, 272$; $P < 0.01$) but not biomass (ANOVA $F = 0.71$; $df = 15, 272$; ns). There was no spatial correlation between potential-prey patterns of numbers or biomass and *M. rapax* density ($r = +0.0008$ ns; $r = 0.36$ ns).

Laboratory experiment results.—The feeding behavior of *M. rapax* confounded the treatment effect in this experiment. After eating the first few (2–4) successive meals, many of the high-food treatment spiders ceased feeding. They often remained at the bottom of their burrow and would not respond for days or weeks. Even though they were offered food, they did not feed. This diluted the differences in food consumed between the two treatments (Table 2). Nevertheless, the total

food consumed by the spiders in the two treatments differed. The high-food treatment spiders ate significantly more and were significantly heavier at the end of the experiment (Table 2). High-food treatment females gained 24% and low-food treatment females lost 4% of initial body weight. High-food treatment females were also significantly less active (less often in foraging position) than low-food females (Table 2). Spider growth was positively correlated with the number of meals eaten ($r = +0.87$; $P < 0.01$). When this relationship is plotted, the "break-even point" or the number of meals eaten over the 11 months that resulted in no weight change was approximately four meals (Fig. 3).

Field experiment results.—Of the 43 spiders in the unmanipulated group, most kept their burrow open through 20 February, but 38% had closed their burrow by 10 March (Fig. 4A). On 10 March, 59% were still active at the top of their burrow. Among the 30 spiders in the food-supplementation group, only 45% had open burrows by 10 March (Fig. 4B). Fewer of the food-supplementation group remained active; by 20 February this proportion of active individuals was significantly lower than among the unmanipulated group (Fig. 4). On 10 March, only 7% of the food-supplementation females were actively foraging, while 60% of the unmanipulated females were active (Fig. 4).

DISCUSSION

Density and dispersion.—One clear result of this study is that the burrows of *M. rapax* are clumped. Clumped dispersion patterns have been observed in a variety other mygalomorph species (Main 1982, 1987; Marples & Marples 1972; Coyle & Icenogle 1994) and
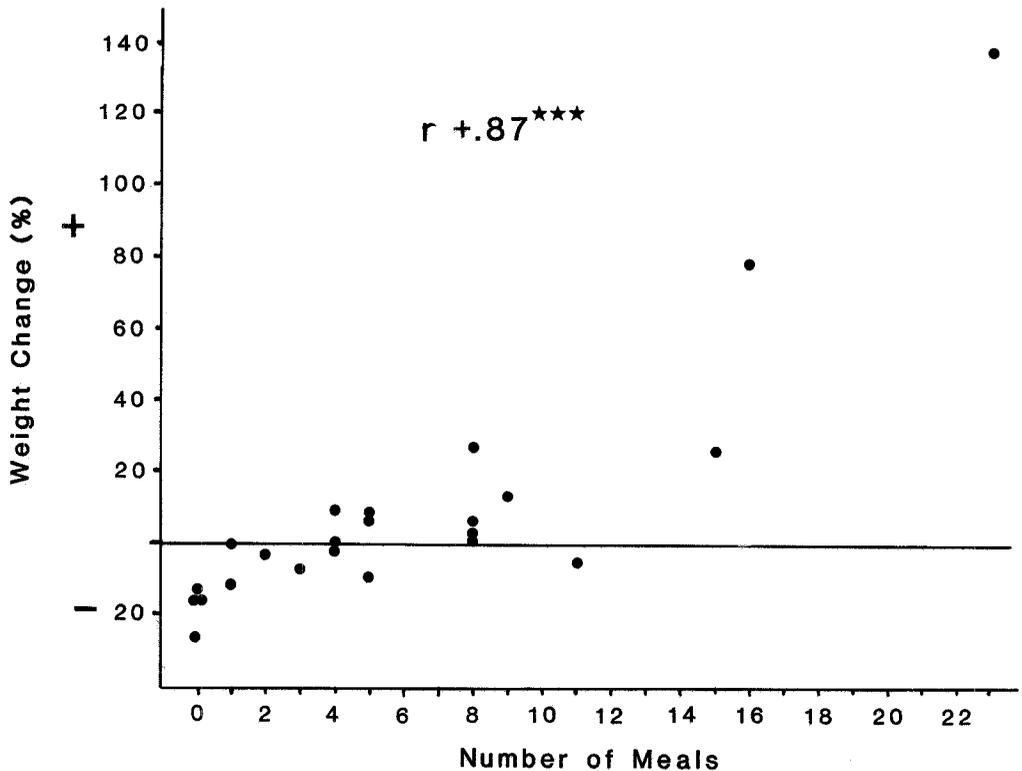
Figure 3.–The weight gained (+) or lost (−) during the laboratory feeding experiment as a percentage of initial spider weight compared to the number of meals eaten by an individual female *M. rapax*. The horizontal line represents no change in weight. These two variables are positively correlated ($r = +0.87$, $P < 0.001$).

burrowing Lycosidae (Humphreys 1976; Fernández-Montraveta et al. 1991). It is possible that the aggregation of *M. rapax* burrows reflects limited dispersal from the maternal burrow, but I observed no tendency for peripheral burrows to be smaller nor a central large burrow indicative of a "matriarch" as described by Main (1978, 1987). It is possible that longevity and relatively low recruitment rates might obscure any such pattern.

The density estimates for *M. rapax* obtained in the current study (391/ha or 0.04/m²) are considerably lower than those published for other large burrowing spiders. Humphreys (1976) indicates that density in *Geolycosa godeffroyi* (L. Koch) was quite variable and locally high in relativley small areas of disturbed or edge habitat. Densities at Humphreys' Kowan study site range between 0.16–1.3 spiders/m² (Humphreys 1976; estimated from his fig. 5). Mature female density was about 0.01/m². *Geolycosa godeffroyi*

is a large spider (mature female mass approximately 1.5 g, Humphreys 1976), but this is equivalent to only 63% of the size of a mature female *M. rapax* (2.4 g, this study Table 2). McQueen (1983b) studied *Geolycosa domifex* (Hancock) and observed extremely variable and high densities (5–13 spiders/m²). The spiders were not uniformly dispersed and average density over the entire field site rarely exceeded 1/m² (McQueen 1983b). Like *Geolycosa godeffroyi*, *G. domifex* is relatively smaller than *M. rapax* (mature female mass *ca.* 0.5 g; McQueen 1983a). One might expect that a large, long-lived mygalomorph such as *M. rapax* would be found at lower densities than the smaller lycosids. Other studies of mygalomorphs, however, have documented high population densities (Marples & Marples 1972; Fairweather 1993; Wishart 1993). Marples & Marples (1972) provide estimates ranging from 1.5–292 spiders/m² for *Cantuaria toddi* Forster in New Zealand. This re-
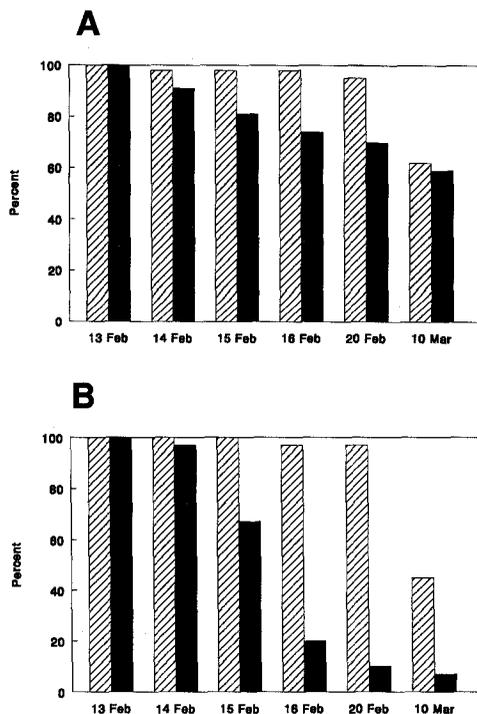
A

B

Figure 4.–The results of the field food-supplementation experiment. The percentage with open burrows (hatched bars) and the percentage where the spider was observed within three cm of the burrow entrance in the foraging position (solid bars) on the four feeding dates (13–16 February 1986) and subsequently on 20 February 1986 and 10 March 1986. (A) The percentage of open burrows and active spiders among unmanipulated (control) spiders, $n = 43$. (B) The percentage of open burrows and active spiders among food-supplemented spiders, $n = 30$.

markable range of densities reflects the fact that the burrows of *C. toddi* were found in dense clusters in restricted habitats such as cliffsides and road margins (Marples & Marples 1972). Fairweather obtained estimates of approximately 0.8–6.4 spiders/m² for *M. rapax* and 4–12 spiders/m² for *Misgolas gracilis* (Fairweather 1993; estimated from his fig. 1). Like Humphreys, Fairweather sampled in habitat patches that were in some cases near ecotones or edges. To some extent the "edge effect" (Leopold 1947) may have influenced the high population density estimates. A similar effect, attributed to remnant habitats and low predator density is cited by Wishart to explain the relatively high population densities of a series of mygalomorph species (Wis-

hart 1993). Oxford (1993) conducted a long term (19 yr) study of local populations of the theridiid *Enoplognatha ovata* (Clerck) and found a consistent pattern of spiders found only near "verges of roads and tracks" mostly near dry-stone walls. A recent review indicates that ecotones support increased biodiversity and productivity (Risser 1995). It is not clear whether this edge effect might also be applied to the current study site which is near two small dirt roads and within ½ km of a major habitat discontinuity.

There was signficant variation in *Misgolas* density across the study area. I detected no signficant correlations between *M. rapax* density and any environmental variables (vegetation variables, slope, soil penetrance) or prey relative-abundance measures. Site-specific variation in density was also demonstrated for *M. rapax* by Fairweather (1993; his table 2). It is relevant to consider the spatial scale of the current study; all 16 study plots were within a patch of habitat 1.5 ha in extent. At this relatively small spatial scale, the observed density variation may reflect stochastic effects magnified by the aggregated dispersion pattern. At larger spatial scales, it is clear that *M. rapax* and other related mygalomorphs exhibit habitat specificity (Fairweather 1993).

One feature of this habitat that has the potential to create patchy distributions is fire. The frequency of fire in this area is relatively high. Main (1981) indicates that adults of fossorial species such as *Anidiops villosus* (Rainbow) survive fire in their burrows. Main (1995) pointed out that the post-fire environment, with reduced shade and litter, was often hostile. Main (1995) suggests that increased adult mortality and declining juvenile recruitment may result in long-term population declines in *A. villosus* after fire. Observations of *M. rapax* after a fire burned this area (in 1987 after the conclusion of this study) indicate that few, if any, individuals were injured. The fossorial habit of this species provided ample protection from fire in the short term. At Brisbane Water National Park plant communities and insects rebounded rapidly after bushfire so the likelihood that variation in prey distribution reflects fire-history is probably low. Fire was shown to have little effect on spider densities or communities in Québec (Koponen 1993) and in Germany (Schaefer 1980).

Activity patterns.—There appears to be

little demonstrable relationship between activity levels of *M. rapax* and proximate weather conditions or seasonality. Activity, as assessed by the proportion of burrows open or spiders near their burrow entrances, was low and unpredictable. This result contrasts with other work on sit-and-wait spiders whose activity levels are influenced by temperature (Buchli 1969; Ford 1978), rainfall, humidity or season (Buchli 1969; Shook 1978; Main 1981). *Misgolas rapax* do appear to forage primarily at night; in this respect it is similar to other trapdoor spiders (Buchli 1969; Coyle 1981) and the theraphosid *Aphonopelma seemanni* (F. P. Cambridge) (Herrero & Valerio 1986). In two species of large burrowing lycosid spiders, no diel periodicity was detected (Humphreys 1973; McQueen & Culik 1981). Other lycosids are strictly nocturnal, e.g., *Lycosa carolinensis* Walckenaer (Shook 1978).

One factor that has been shown to influence burrow closure in trapdoor spiders is rainfall (McKeown 1936; Main 1993). Foraging activity of *M. rapax* during rainstorms was very low, but insufficient data were collected during storms to evaluate this observation statistically. There is no indication in the data that more *M. rapax* burrows were found closed immediately after rainstorms. The soils in this study area are sandy and well drained. Even though the soil is occasionally saturated after heavy rain, there is little chance that standing water would persist. Main has suggested that one of the primary functions of the closable sock in the open burrows of *Misgolas* is to prevent flooding of the burrow (Main 1993).

There is no evidence that daily activity levels, seasonal activity patterns or population densities of *M. rapax* are responsive to variation in prey availability. On the other hand, results from the laboratory and field food-supplementation experiments indicate that well-fed individuals are significantly less active. One explanation for the lack of correspondence between spider activity and prey phenology is that prey availabiliy was not accurately measured by pitfall traps. Evidence against this interpretation is that the pitfall traps captured all of the known prey species, and that when pit data were altered to include only known prey species, there was even less relationship to spider activity patterns. It should be noted that I have little information about the proportions of prey in the natural diet of *M. rapax*. Thus, it is still possible that a subtle positive relationship between prey availability and spider activity exists which could not be detected by the methods I employed in this study.

A second plausible explanation for the results I obtained is that prey are too unpredictable in time and space to be tracked by variation in spider activity. Sedentary burrowing trapdoor spiders only detect prey a limited distance from their burrows (Main 1957; Buchli 1969). Perhaps the encounter rates with prey are too infrequent, and the variation in prey availability is too irregular for *M. rapax* to have evolved a mechanism that could predict prey encounters. In his review of foraging strategies of spiders, Uetz (1992) explains that in cases where differences in the fitness gain between behavioral strategies are small, one might not expect the evolution of a single optimum strategy.

Another explanation for the lack of a correspondence between activity patterns of *M. rapax* and potential prey is that the annual food requirements are so low that this effect is undetectable. As few as four meals/yr are sufficient for maintenance of body weight, and individuals consuming 20 meals/yr can double their body weight (Fig. 3). Many individuals provided with a few supplemental prey in the field experiment closed their burrows and/or became inactive. *Misgolas rapax* were shown to have extraordinarily long periods of inactivity in the field ($\bar{x}$ = 76 days) and may live many years as has been shown for other members of the family (Main 1981, 1982). Variation in prey availability as measured by the pitfall samples was evident from month-to-month, but with only a weak seasonal pattern. It seems that the temporal scale of variation in prey is too short relative to the patterns of activity/aestivation in *M. rapax*.

One last factor that may exert a powerful influence on activity of *Misgolas* is the risk of predation. It is possible that the long periods of burrow closure are a response to the risk of predation. Both of the chief predators of this species (wasps and legless lizards) enter burrows to attack *M. rapax*. Predatory wasps (Sphecidae, Pompilidae) which prey on spiders commonly inhabit the area of the current study. A large pompilid *Cryptochelius* (sp.?) was commonly observed hunting near the ground in the study area and is a potential

predator of *Misgolas*. One of the chief predators of *M. rapax* is the legless lizard *Pygopus lepidopodus* (Lacépède) (Patchell & Shine 1986). This species has been commonly observed on the study site, is broadly sympatric with *M. rapax* (Cogger 1983), and may be specialized for hunting large burrowing spiders (Shine 1986). Both *Pygopus lepidopodus* and the predatory wasps are diurnal or crepuscular. It is by no means certain that these predators influence the activity patterns of *M. rapax*, but this subject deserves further study.

I studied *M. rapax* at the same time and at the same locality as I conducted work on the orb-weaver *Argiope keyserlingi*. While *A. keyserlingi* density was directly related to measurable features of the vegetation (Bradley 1993), density of *M. rapax* was not. The simplest explanation for this difference is that *Argiope* actually use the vegetation as a framework to construct their snares. Local aggregations of *Misgolas* appear to reflect limited dispersal of juveniles and long persistance of individuals. Neither species appears to exhibit activity or density patterns that reflect prey availability. For both species the availability of prey appears to be unpredictable in both space and time. At larger spatial scales, there is no doubt that these spiders have habitat preferences (Fairweather 1993; Levi 1983).

ACKNOWLEDGMENTS

LITERATURE CITED

Bradley, R. A. 1986. The relationship between population density of *Paruroctonus utahensis* (Scorpionida: Vaejovidae) and characteristics of its habitat. J. Arid Environ., 11:165–171.

Bradley, R. A. 1993. The influence of prey availability and habitat on activity patterns and abundance of *Argiope keyserlingi* (Araneae: Araneidae). J. Arachnol., 21:91–106.

Buchli, H. H. R. 1969. Hunting behavior in the Ctenizidae. American Zool., 9:175–193.

Cogger, H. G. 1983. Reptiles and Amphibians of Australia. A. H. & A. W. Reed, Frenchs Forest, NSW, Australia.

Conley, M. R. 1985. Predation versus resource limitation in survival of adult burrowing wolf spiders (Araneae: Lycosidae). Oecologia, 67:71–75.

Coyle, F. A. 1981. Notes on the behaviour of *Ummidia* trapdoor spiders (Araneae, Ctenizidae): burrow construction, prey capture, and the functional morphology of the peculiar third tibia. Bull. British Arachnol. Soc. 5:159–165.

Coyle, F. A. & W. R. Icenogle. 1994. Natural history of the Californian trapdoor spider genus *Aliatypus* (Araneae, Antrodiaetidae). J. Arachnol., 22:225–255.

Fairweather, P. G. 1993. Abundance and structure of fossorial spider populations. Mem. Queensland Mus., 33:513–518.

Fernández-Montraveta, C., R. Lahoz-Beltra, & J. Ortega. 1991. Spatial distribution of *Lycosa tarentula fasciiventris* (Araneae, Lycosidae) in a population from central Spain. J. Arachnol., 19:73–79.

Ford, M. J. 1978. Locomotory activity and the predation strategy of the wolf-spider *Pardosa amentata* (Clerck) (Lycosidae). Anim. Behav., 26:31–35.

Herrero, M. V. & C. E. Valerio. 1986. Analisis de la actividad diaria de *Aphonopelma seemanni* (Araneae, Theraphosidae) en Costa Rica. J. Arachnol., 14:79–82.

Humphreys, W. F. 1973. The environment, biology and energetics of the wolf spider *Lycosa godeffroyi* (L. Koch 1865). Ph.D. thesis, Australian Nat. Univ., Canberra.

Humphreys, W. F. 1976. The population dynamics of an Australian wolf spider, *Geolycosa godeffroyi* (L. Koch 1865) (Araneae: Lycosidae). J. Anim. Ecol., 45:59–80.

Kershaw, K. A. 1973. Quantitative and Dynamic Plant Ecology, 2nd ed. Arnold, London.

Koponen, S. 1993. Ground-living spiders (Araneae) one year after fire in three subarctic forest

types, Québec (Canada). Mem. Queensland Mus., 33:575–578.

Lamoral, B. H. 1978. Soil hardness, an important and limiting factor in burrowing scorpions of the genus *Opisthophthalmus* C. L. Koch, 1837 (Scorpionidae, Scorpionida). Symp. Zool. Soc. London, 42:171–181.

Leopold, A. 1947. Game Management. Charles Scribner's Sons, New York.

Levi, H. W. 1983. The orb-weaver genera *Argiope*, *Gea*, and *Neogea* from the western Pacific region (Araneae: Araneidae, Argiopinae). Bull. Mus. Comp. Zool., 150:247–338.

Main, B. Y. 1957. Biology of Aganippine trapdoor spiders (Mygalomorphae: Ctenizidae). Australian J. Zool., 5:402–473.

Main, B. Y. 1978. Biology of the arid-adapted trapdoor spider *Anidiops villosus* (Rainbow). Bull. British Arachnol. Soc., 4:161–175.

Main, B. Y. 1981. Australian spiders: Diversity, distribution and ecology. Pp. 808–852, *In* Ecological Biogeography of Australia (A. Keast, ed). v. 2. W. Junk, The Hague.

Main, B. Y. 1982. Adaptations to arid habitats by Megalomorph spiders. Pp. 273–283, *In* Evolution of the flora and fauna of arid Australia. (W. R. Barker & P. J. M. Greenslade, eds.). Peacock Publications, Frewville.

Main, B. Y. 1984. Spiders. Collins, Sydney.

Main, B. Y. 1987. Persistence of invertebrates in small areas: case studies of trapdoor spiders in Western Australia. Pp. 29–39, *In* Nature conservation: the role of remnants of native vegetation. (D. A. Saunders, G. W. Arnold, A. A. Burbridge, & A. J. M. Hopkins, eds.). Surrey Beatty & Sons, Sydney.

Main, B. Y. 1993. From flood avoidance to foraging: adaptive shifts in trapdoor spider behaviour. Mem. Queensland Mus., 33:599–606.

Main, B. Y. 1995. Survival of trapdoor spiders during and after fire. CALM Sci. Suppl., 4:207–216.

Marples, B. J. & M. J. Marples. 1972. Observations on *Cantuaria toddi* and other trapdoor spiders (Aranea: Mygalomorpha) in Central Otago, New Zealand. J. Royal Soc. New Zealand, 2:179–185.

McKeown, K. C. 1936. Australian Spiders. Angus & Robertson, Sydney.

McQueen, D. J. 1983a. Field studies in growth, reproduction, and mortality in the burrowing wolf spider *Geolycosa domifex* (Hancock). Canadian J. Zool., 56:2037–2049.

McQueen, D. J. 1983b. Mortality patterns for a population of burrowing wolf spiders, *Geolycosa domifex* (Hancock), living in southern Ontario. Canadian J. Zool., 56:2758–2767.

McQueen, D. J. & B. Culik. 1981. Field and laboratory activity patterns in the burrowing wolf spider *Geolycosa domifex* (Hancock). Canadian J. Zool., 59:1263–1271.

Oxford, G. S. 1993. Components of variation in population size in the spider *Enoplognatha ovata* (Clerck) sensu stricto (Araneae: Theridiidae). Bull. British Arachnol. Soc. 9:193–202.

Patchell, F. C. & R. Shine. 1986. Food habits and reproductive biology of the Australian legless lizards (Pygopodidae). Copeia, 1986:30–39.

Polis, G. A. & S. J. McCormick. 1986. Patterns of resource use and age structure among a guild of desert scorpions. J. Anim. Ecol., 55:59–73.

Risser, P. G. 1995. The status of the science: examining ecotones. BioScience, 45:318–325.

Rogers, L. E., W. T. Hinds & R. L. Buschbom. 1976. A general weight vs. length relationship for insects. Ann. Entomol. Soc. America, 69:387–389.

Rogers, L. E., R. L. Buschbom & C. R. Watson. 1977. Length-weight relationships of shrub-steppe invertebrates. Ann. Entomol. Soc. America, 70:51–53.

Schaefer, M. 1980. Effects of an extensive fire on the fauna of spiders and harvestmen (Araneida and Opilionida) in pine forests. Proc. 8th Intern. Cong. Arachnol., Vienna; pp. 103–108.

Shine, R. 1986. Evolutionary advantages of limblessness: evidence from the pygopodid lizards. Copeia, 1986:525–529.

Shook, R. S. 1978. Ecology of the wolf spider, *Lycosa carolinensis* Walckenaer (Araneae, Lycosidae) in a desert community. J. Arachnol., 6:53–64.

Southwood, T. R. E. 1966. Ecological Methods. Methuen & Co., London.

Wishart, G. F. C. 1993. The biology of spiders and phenology of wandering males in a forest remnant (Araneae: Mygalomorphae). Mem. Queensland Mus., 33:675–680.

Uetz, G. W. 1992. Foraging strategies of spiders. Trends Ecol. Evol., 7:155–159.