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EFFECT OF RIVER FLOW MANIPULATION ON WOLF SPIDER ASSEMBLAGES AT THREE DESERT RIPARIAN SITES

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ABSTRACT. The distribution, abundance, and diversity of wolf spider (Lycosidae) assemblages were investigated via pitfall trapping at three sites near Granite Reef Dam outside Phoenix, Arizona. These three sites featured different moisture and temperature regimes due to the dam, which diverts the Salt River into an urban canal system. Site 1 was a natural riparian area above the dam along the Salt River, Site 2 was adjacent to a man-made diversion canal, and Site 3 was adjacent to the dry riverbed below the dam. Four lycosid species were found at Site 1, with *Pardosa vadosa* Barnes 1959 dominating. Two species each, though very few total individuals, were found at Sites 2 and 3. Simpson's index of diversity (of lycosids and of all other terrestrial arthropods) was higher for Site 1 than for Sites 2–3. Prey availability was comparable among sites, but Site 1 had significantly higher relative soil moisture levels and less extreme substrate and air temperature conditions than did Sites 2 and 3. Spider abundance at each site was independent of prey availability, but instead depended chiefly upon moisture and temperature regimes among sites. The results suggest that wolf spiders experienced a significant effect from disturbance of their habitat by the dam, and that abiotic habitat attributes such as moisture and temperature may be more important for wolf spider abundance than prey availability alone in desert riparian systems.

Keywords: *Pardosa*, Salt River, Arizona

In comparison to habitats featuring less human impact, urbanization can have significant effects on the environmental conditions, populations, and community structures of ecological systems (McDonnell et al. 1997). While vertebrate populations often may decline due to the anthropogenic pressures and habitat loss associated with urbanization (for example: Hoi Leitner 1989; Gill & Williams 1996), many invertebrate species exhibit an ability to establish alternative ecological relationships allowing them to persist or even flourish in urban environments (Frankie & Ehler 1978; Dreistadt et al. 1990). As a result, arthropod populations and assemblages may be similar among natural and disturbed sites (Frankie & Ehler 1978). As one might expect, however, urbanization has also been shown to have adverse effects on some invertebrate populations (Nowakowski 1986; Sawoniewicz 1986; Ruszczyk & Mellender 1992). Frankie & Ehler (1978) point out that perhaps one of the few generalizations which can be made about terrestrial invertebrate populations in urban environments is that the distribution and diversity of such species often reflect different moisture regimes.

As part of the newly-funded Urban Long Term Ecological Research site in central Arizona, we set out to compare the distribution and diversity of assemblages of wolf spiders (Lycosidae) in three Sonoran Desert riparian areas featuring different environmental regimes as a function of river flow manipulation. We sought to investigate the relationships between wolf spider distribution and abundance patterns to prey availability, temperature regimes (air temperature, substrate temperature, and variation between the two), and relative soil moisture.

Most wolf spiders do not build webs, but rather are vagrant hunters, and spend most of their time near the ground surface. They may wander or remain stationary while hunting until a prey item is detected by visual or vibratory cues, at which point they attack (Kaston

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1978; Kronk & Riechart 1979; Cady 1984; Persons & Uetz 1996). Different species of *Pardosa*, the dominant genus found in this study, have been variously described as either sit-and-wait or cursorial hunters (Morse 1997). A large body of research has demonstrated that wolf spiders exhibit habitat selection and distribution and abundance patterns based on a variety of factors, including: prey availability, capture efficiency, mating probability (in males), herbaceous vegetation cover, temperature, humidity, and soil moisture content (e.g., Cherrett 1964; Hallander 1967, 1970; Lowrie 1973; Kronk & Riechert 1979; Bultman 1992; Cady 1984; Moring & Stewart 1994). Microenvironmental factors such as vegetation cover, temperature, humidity, and prey availability can be directly related to substrate moisture levels.

Based on these studies, we expected that mid-summer censuses (when the abiotic conditions of the desert were at their most extreme) would result in wolf spider assemblages that varied as a function of habitat. In particular, we expected wolf spider abundance and species diversity to depend sensitively on soil moisture as in Kronk & Reichert's (1979) study of *Rabidosa santrita* (Chamberlin & Ivie 1935) and as in Agnew & Smith's (1989) study of spiders in irrigated and drought-stressed peanut fields. Experiments demonstrating the inability of *Pirata piraticus* (Clerck 1757) to tolerate desiccation (Cherrett 1964), as well as the association of many western *Pardosa* species with moist habitats (Lowrie 1973) further supported our expectations.

STUDY SITES AND METHODS

The study sites were two desert riparian areas adjacent to the Salt River and one area along a canal, running through Tonto National Forest near Granite Reef Dam, 22 km east of downtown Phoenix, Arizona. Completed in 1908, Granite Reef Dam is the point where the Salt River is diverted into man-made canals for eventual human use (Higgs 1995). The presence of this water resource is one of the key factors that has facilitated explosive growth of the Phoenix metropolitan area in the last several decades. Because of the river diversion, the riverbed below the dam is nearly completely dry for much of the year. Prior to the completion of Granite Reef Dam, downstream reaches were well-watered and featured desert riparian vegetation typical of upstream areas today (see below). However, Granite Reef Dam is only the most recent modification to the river and surrounding riparian corridor: this portion of the river was also the site of large-scale water diversions into irrigation canals by the Hohokam culture (AD 700–1450) (Gregory 1991).

Site 1 was a strip of riparian area approximately 7 km upstream of the dam in a semi-natural area designated for recreational use. Immature willow (*Salix gooddingii* and *Salix exigua*), cottonwood (*Populus fremontii*), and tamarisk (*Tamarix* spp.; invasive exotics) trees as well as understory riparian vegetation grew along the river bank; the substrate was primarily rock cobble and sand. Site 2 was about 2 km downstream of the dam adjacent to one of the diversion canals. Because the canals were constructed of concrete, which allows for little lateral movement of water outward from the sides of the canal, plant cover at this site, even that immediately adjacent to the canal, was typical upper Sonoran Desert vegetation featuring saguaro cactus (*Carnegia gigantea*) and palo verde *(Cercidium microphyllum)*. The substrate was primarily densely packed sand. Site 3 was an area about 0.5 km downstream of the dam running along the dry riverbed where the river formerly flowed. It featured a mixture of upper Sonoran vegetation and riparian species able to persist on the water and disturbance regime provided by low-volume, irregular releases of water from the dam; the substrate was primarily a mixture of sand and cobbles.

At two locations in each of the three sites, we placed a set of ten pitfall traps (spaced 2 m apart in two rows of five) with the first row located about 2 m away from the adjacent water source (or edge of dry riverbed) and running parallel to it. Traps (plastic drinking cups [''Dixie™''] 9 cm in diameter) were buried in the ground with the rim set flush with the surface. A second cup, with the top 3 cm cut off, was placed in each buried cup for periodic removal of specimens. Forest service regulations, concerns over public access (especially pets), and the intense heat and evaporative potential of the Sonoran Desert region during the summer, mandated that we use ''dry'' pitfall traps (e.g., Hurd & Fagan 1992) rather than traps containing chemical preservatives. To provide a vertical dimension to the trap (and thus refugia for captured animals), we placed a loosely crumpled piece of toweling paper in the bottom of each trap. Trapped spiders and other arthropods were collected every 3–6 days. Spiders were sorted to species (using Kaston 1978 and Roth 1993), and broken down into age (sub-adult, adult) and sex categories. Species identifications based on representative specimens were established by Dr. David Richman (New Mexico State University). Voucher specimens have been deposited in the Central Arizona Phoenix LTER's arthropod collection, which is associated with other natural history collections at Arizona State University (ASU). Other arthropods were sorted to family or order, as possible. We also used dry cup pitfall trapping to provide an estimate of available prey, which included counting all soft-bodied arthropods that did not exceed the average length of the largest wolf spider species found (as in Moring & Stewart 1994). This means that we counted only small, immature, and soft-bodied individuals of Formicidae, Dermaptera, and Coleoptera. Our estimate of available prey thus may be an underestimate for large bodied wolf spiders that have sometimes been observed feeding on hard-bodied insects (e.g., Coleoptera, Orthoptera [Nyffeler & Benz 1988]). Although the inability of lycosids to climb up the smooth surfaces of pitfall traps does not preclude the use of dry pitfall trap data for wolf spiders, many potential insect prey may walk or fly out of such traps or be preyed upon by lycosids while in the traps, which means that our arthropod data are likely underestimates.

Traps were in place from 11 June 1998–13 July 1998, although a rising river level behind the dam (due to early arrival of the monsoon season in the Sonoran Desert) washed out all traps at Site 1, forcing the early termination of arthropod collection on 30 June 1998 at that site. After finding (1) no discernable differences between trapped arthropods at Sites 2 and 3 between the periods 11 June–30 June 1998 and 30 June–13 July 1998 and (2) no temporal trends in abundance at Site 1, we corrected for the different numbers of trap days by multiplying all counts at Site 1 by 32/17. Our results are comparable if we restrict our analyses to data taken from all three sites between 11 June–30 June 1998. Temperature readings were taken at selected locations near each set of traps at each site over four non-consecutive, sunny days, with four readings being taken at each plot every hour between the hours of 0700–1100 h. Both ground temperatures and air temperatures (with the thermometer held 2 cm above the ground) were taken. Soil moisture readings were taken with a soil moisture probe (measuring relative percent soil moisture) on one day with five measurements being taken at Sites 2 and 3. Six readings were taken at Site 1 (three at each sub-site) as more variable soil moisture levels were found.

RESULTS

Pardosa vadosa Barnes 1959 was by far the most common lycosid in the vicinity of Granite Reef Dam, comprising well over 90% of the individual lycosids captured (Table 1). *Pardosa vadosa* (5–6 mm as adults) was also the only lycosid found at all three sites. For this species, 54% of the mature, identifiable individuals were female, indicating a relatively balanced sex ratio during the sampling period. In addition, *P. vadosa* was the only species for which a large number of sub-adults was collected. This is potentially important because it could indicate that other lycosids may reproduce at different times of the year than *P. vadosa*, which could lead to markedly different abundance patterns through time. *Arctosa littoralis* (Hentz 1844) (adult size 12–15 mm), which was found only at Site 1, was the next most common lycosid as determined by pitfall trap collections. *Sosippus californicus* Simon 1898 (adult size 12–16 mm) was also found only at Site 1, but in low numbers. *Allocosa subparva* Dondale & Redner 1983 (adult size 4–5 mm) was found at both Sites 1 and 3, but in low numbers at the latter site, while *Pardosa* sp. #2 was found only at Site 2, again in low numbers. After lycosids, the Gnaphosidae was the next most common family of spiders caught in the pitfall traps.

Pitfall trapping indicated wolf spiders were more abundant at Site 1 than at Sites 2–3 (Table 1). This pattern held for male, female, sub-adult, and unidentifiable individuals (sex unidentifiable due to severe desiccation and/or cannibalism in traps). Roughly 16% of collected wolf spiders appeared to have been attacked by other spiders while inside the dry pitfall traps.

Other arthropods commonly represented at

Table 1.—Total counts of each arthropod group at each site, with lycosids separated into species. All Site 1 traps were destroyed on day 18. Site 1 specimen counts are corrected for differential trap-days by multiplying by 32/17.

	Site 1-A*	Site 1-B*	Site 1 (pooled*)	Site 2-A	Site 2-B	Site 2 (pooled)	Site 3-A	Site 3-B	Site 3 (pooled)
Lycosidae									
Pardosa vadosa (total)	602	652	1254	3	0	3	0	2	2
Female	171	168	339	2	0	2	0	1	1
Male	139	149	288	0	0	0	0	0	0
Sub-adult	136	288	424	1	0	1	0	1	1
Sex unidentifiable	156	47	203	0	0	0	0	0	0
Pardosa sp. 2 (total)	0	0	0	3	0	3	0	0	0
Female	0	0	0	0	0	0	0	0	0
Male	0	0	0	0	0	0	0	0	0
Sub-adult	0	0	0	3	0	3	0	0	0
Arctosa littoralis (total)	32	10	42	0	0	0	0	0	0
Female	11	6	17	0	0	0	0	0	0
Male	19	4	23	0	0	0	0	0	0
Sub-adult	0	0	0	0	0	0	0	0	0
Sex unidentifiable	2	0	2	0	0	0	0	0	0
Allocosa subparva (total)	14	0	14	0	0	0	0	1	1
Female	6	0	6	0	0	0	0	1	1
Male	6	0	6	0	0	0	0	0	0
Sub-adult	0	0	0	0	0	0	0	0	0
Sex unidentifiable	2	0	2	0	0	0	0	0	0
Sosippus californicus (total)	6	2	8	0	0	0	0	0	0
Female	2	2	4	0	0	0	0	0	0
Male	4	0	4	0	0	0	0	0	0
Sub-adult	0	0	0	0	0	0	0	0	0
Gnaphosidae	9	21	30	16	2	18	0	2	2
Salticidae	0	0	0	1	0	1	1	4	5
Clubionidae	0	2	2	1	1	2	0	0	0
Oxyopidae	0	0	0	1	0	1	0	0	0
Theridiidae	0	0	0	0	0	0	1	3	4
Unknown spiders	2	0	2	11	10	21	4	8	12
Formicidae	1020	446	1466	521	782	1303	1298	1193	2491
Coleoptera	200	597	797	126	163	289	107	171	278
Isopoda	1316	85	1401	39	7	46	30	35	65
Acarina	2	184	186	74	55	129	132	60	192
Collembola	0	0	0	78	100	178	11	25	36
Dermaptera	171	32	203	0	0	0	0	0	0
Scorpiones	0	21	21	5	25	30	9	7	16
Miscellaneous available prey	2	17	19	43	26	69	9	31	40
Total available prey	1067	632	1699	625	708	1333	1258	1121	2379

these sites included members of the taxa: Formicidae, Isopoda, Coleoptera, Acarina, Collembola, Dermaptera, and Scorpiones. Formicids comprised the dominant group at all sites. Kendall's rank correlation analyses of the relative abundance of the top ten arthropod groups found at each subsite indicated greater intrasite variability at Site 1 than at Sites 2–3 (Table 2). In addition rank correlation analyses indicated substantial differences in relative abundance of different arthropod groups between Site 1 and Sites 2–3. However, Sites 2–3 harbored strikingly similar arthropod assemblages overall (Table 2).

Table 2.—Rank correlation coefficients for arthropod assemblages within and among pitfall sampling sites. Analyses involve the 10 most common arthropod groups except for analyses involving Site 3 in which only 9 groups were sufficiently common for analysis. * = significant at $P = 0.05$, ** = significant at $P = 0.01$.

Sites compared	Rank correlation coefficient
Sub-sites at Site 1:	0.547*
Sub-sites at Site 2:	0.786**
Sub-sites at Site 3:	0.983**
Site 1 vs. Site 2:	0.442
Site 1 vs. Site 3:	0.569
Site 2 vs. Site 3:	0.940**

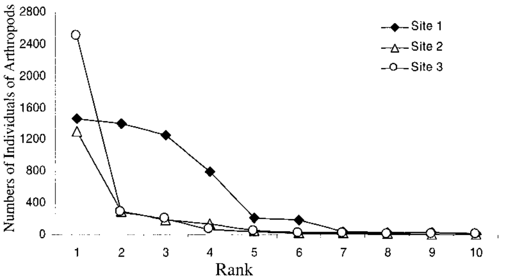

Figure 1.—Dominance diversity curves of the 10 most abundant groups of arthropods at each site. Counts from Site1 are sums of actual and projected counts.

Dominance-diversity curves (Fig. 1) also reveal striking differences among sites. Arthropod collections at Site 1 are dominated by four groups of arthropods (Formicidae, Isopoda, *Pardosa vadosa*, and Coleoptera), whereas Formicidae are clearly dominant at Sites 2 and 3. Calculating Simpson's index of diversity also indicates higher terrestrial arthropod diversity at Site 1 (0.781) compared with Sites 2 and 3 (0.553 and 0.349, respectively). Wolf spider abundance at each site showed no correlation with available prey (Kendall's rank correlation; Fig. 2). Total wolf spiders collected at Site 1 far exceeded those collected at Sites 2 and 3, but available prey varied only slightly between sites.

Average morning air and substrate temperatures at Site 1 were lower than comparable averages from Sites 2 and 3 (MANOVA, Wilks' Lambda = 0.572, $P < 0.001$). In addition, substrate temperatures at Sites 2 and 3 were on average 2.4 °C and 1.5 °C higher, respectively, than corresponding air temperatures, while at Site 1 (the natural river site) average air and substrate temperatures were virtually identical. At Site 1, substrate temperatures on the cobblestones were generally warmer than the air and the soil was generally cooler. The relative abundance of lycosids decreased as air temperature, substrate temperature, and the temperature difference between air and substrate increased (Fig. 3). Relative abundance of wolf spiders also increased with increasing relative soil moisture among sites. At Site 1, where relative soil moisture ranged from 50–70%, wolf spiders represented between 20–35% of the pittrap-collected fauna. In contrast, at Sites 2 and 3, where relative soil moisture ranged from 0–10%, wolf spiders represented less than 2% of the pittrapped specimens.

DISCUSSION

Overall, abiotic conditions and the diversity of available prey appear to influence wolf spider diversity and abundance in riparian and pseudo-riparian areas near Granite Reef Dam in central Arizona. In particular, the less extreme moisture and temperature regimes of the riparian habitat at Site 1 likely facilitated the greater abundance of wolf spiders there. Although substrate temperature was consistently higher than air temperature at Sites 2 and 3, substrate temperature differed little from air temperature at Site 1, where high soil moisture levels likely contributed to a cooling effect. Experimental studies of microhabitat

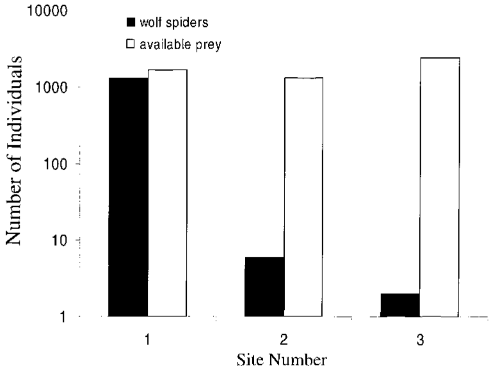

Figure 2.—Total lycosids trapped at each site compared to total available prey. Available prey included all soft-bodied arthropods that did not exceed the average length of the largest wolf spider species found. Note logarithmic y-axis.

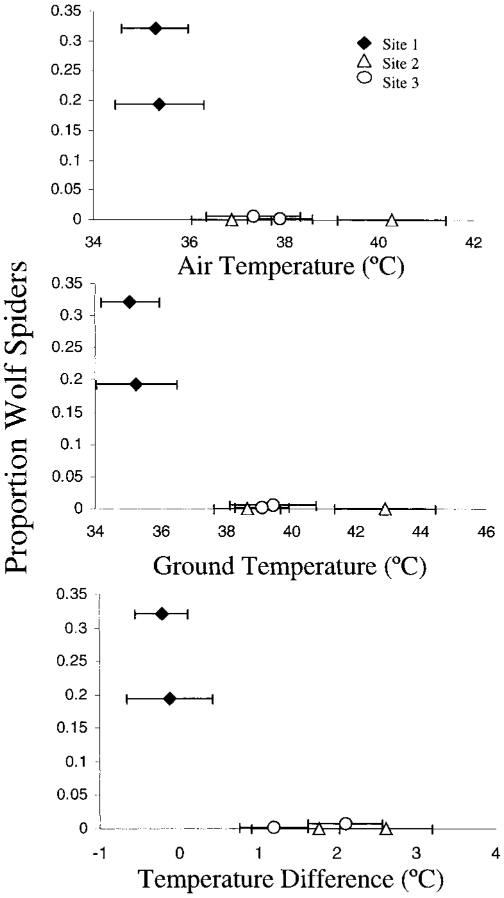

Figure 3.—The proportion of wolf spiders (all species) at each sub-site as a function of temperature regimes. Temperature readings were taken in early to mid-morning, before the most thermally-oppressive part of the day. Air temperature was taken approximately 2 cm above the ground surface. Error bars give standard errors of temperature readings.

selection at Site 1 could support or refute the idea that spiders are actually selecting the riverside for (at least in part) its less extreme temperatures.

Wolf spider abundance and diversity were also positively related to relative soil moisture among sites. These results agree strongly with our prediction that we would find the greatest abundance and diversity of wolf spiders by the natural river upstream of the dam, due to the importance of proximity to water and moist soil for lycosid distributions (Cherrett 1964; Kronk & Riechert 1979; Cady 1984; Agnew & Smith 1989; Bultman 1992). Indeed, Lowrie (1973) has shown that moisture is a key factor in the fairly specific habitat preferences of many species of *Pardosa*, the dominant genus found in this study.

In general, prey availability has been shown to be an important aspect of spider habitat association (Kronk & Riechert 1979; Moring & Stewart 1994; Henshel & Lubin 1997). But, because wolf spiders are known to require a variety of food items in order to reach maturity (Uetz et al. 1992), higher species diversity at Site 1 as opposed to the overall abundance of prey species (Fig. 2) may contribute to increased wolf spider abundance there. Similar plant species composition at Sites 2 and 3 likely contributes to the strong rank correlation among groups of arthropods between those sites, especially with respect to herbivorous insects (Table 2).

All analyses of prey availability, however, must be viewed in the light that pitfall trapping is a sampling method with differential capture success among species. For instance, pitfall traps sample not the true density, but rather the ‘‘active density’’ of wandering arthropods in an area over a given time (Uetz & Unzicker 1976; Uetz 1977). The dry pitfall traps likely under-sampled potential insect prey, as mentioned above, especially Diptera, which may comprise a significant component of *Pardosa* diet (Hallander 1970; Morse 1997; Nyffeler & Benz 1988; Nyffeler & Breene 1990). Predation by the numerous spiders in the dry traps at Site 1 may also have reduced prey availability at that site, possibly accounting for the similarity in prey abundance collected at each site. Pitfall traps are still useful, however, in estimating the number of species of wandering spiders present over a wide range of habitats (Uetz & Unzicker 1976).

Although we lack data on spider distributions prior to dam construction, the results of this study suggest that wolf spider assemblages may have been substantially affected by dam construction, water diversion, and subsequent changes of the riparian vegetation in the vicinity of Granite Reef Dam. Our results support the hypotheses that desert riparian wolf spider-habitat associations are strongly influenced by soil moisture and substrate-air temperature regimes and that abundance of available prey alone may not be a good predictor of wolf spider distributions.

The impacts of urbanization on spider assemblages are worth investigating because spiders are not only an important food source for birds, lizards, wasps, and other species; but, when viewed as an assemblage of generalist predators, they may also play an important role in the regulation of insect populations (Riechert & Lockley 1984; Settle et al. 1996; Morse 1997; Skerl 1997). Overall, the study of the ecological consequences of urbanization for particular groups of plants and animals is important because it can indicate the degree of disturbance of their environments and may be useful in developing strategies for conservation (Ruszczyk & Mellender 1992). Although this research was specifically designed as a summer study, when the desert environment was at its most extreme, it would be interesting to investigate if the striking patterns observed here persist within and among years, when the desert riparian sites experience a greater range of environmental conditions.

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