

CONDITIONS FAVORING GROUP LIVING IN WEB-BUILDING SPIDERS IN AN EXTREME DESERT ENVIRONMENT

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ABSTRACT

Colonial spiders construct individual capture webs within a matrix of shared supporting frame threads. *Cyrtophora citricola* is a colonial orb-weaving spider with a complex three-dimensional web. Colonies may contain a few to several hundred individuals, but individuals may also occur solitarily. Local conditions such as food supply and substrate availability are likely to influence colony formation. In this study we explored the influence of local conditions and dispersal behavior on colony establishment in a desert population of *C. citricola* in the hyper-arid Arava Valley in Israel. Colonies in the Arava occur primarily on scattered *Acacia* trees and less commonly on shrubs. The spatial distribution of colonies was clustered and was not influenced by the condition of the *Acacia* trees (leaf flush, flowering, or fruiting). In a controlled experiment, we showed that dispersing spiders remained longer and built webs faster in trees that contained conspecific webs than in trees without webs. We propose that spiders benefit from establishing webs in the proximity of other spiders, while dispersal to another tree may not result in arrival at an improved habitat. These two factors may promote colony living even in prey-poor environments such as the extreme desert.

Keywords: Dispersal, colony living, *Cyrtophora citricola*, Araneidae, *Acacia*, Arava Valley

INTRODUCTION

For group-living animals, the decision to disperse from the parental site depends on a combination of ecological constraints on independent breeding (e.g., resource availability and patch size) and the costs and benefits of group living. The main benefit of dispersal is the possibility of reaching a rich patch that is free from competition for essential resources. Nevertheless, it would be beneficial for the organism to delay or forego dispersal and stay at the parental site if (1) the available patches are of poor quality, (2) most

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Received 11 October 2009, accepted 23 May 2010.

of the suitable patches are already occupied (“habitat saturation”), or (3) the probability of finding a mate away from the natal site is low (Koenig and Pitelka, 1992; Emlen, 1994). Theory suggests that once group living has evolved as a consequence of ecological constraints, secondary benefits of staying may become important and will reinforce philopatry (Lindström, 1986; Emlen, 1994). Secondary benefits include protection from predators, increased probability of inheriting the parent site, indirect fitness gains from cooperating with other family members, and better opportunities to secure a nearby, high quality breeding site in the future (Emlen, 1994). However, there are also costs to group living that could induce individuals to breed independently even when ecological constraints are present. These costs include increased disease and parasite transmission, competition for resources, and the risk of inbreeding (Krause and Ruxton, 2002).

Group living has evolved most often in species living in habitats rich in food (Uetz and Hieber, 1997). Abundance of food reduces the cost of competition for resources and increases the benefits of group foraging. Group foraging can also be a risk-averse strategy, by reducing the variance in food acquired by an individual, particularly when high quality resources are patchy (Krause and Ruxton, 2002). Thus, social structure may vary from solitary to group living depending on the spatial and temporal distribution of food (Emlen, 1994). In some species, it was shown that group living is a flexible trait (e.g., the spider *Achaearanea tepidarorium*: Rypstra, 1986; Seychelles warbler, *Acrocephalus sechellensis*: Komdeur, 1992). This flexibility may be an outcome of different equilibria between ecological constraints and benefits and costs of group living. In this study, we investigated the environmental conditions that influence grouping in a web-building spider living in an extreme, resource-poor desert environment.

Colonial web building spiders have flexible group sizes. They may live solitarily or in groups depending on the local context (Uetz and Heiber, 1997; Lubin, 2010). Colony members maintain individual webs that are defended against conspecifics, but they share frame threads to anchor individual webs and in some species they may even share large prey (Fernández Campón, 2007, 2008). The benefits of group living include greater web-building efficiency with reduced silk costs, greater efficiency in prey capture (especially of large insects), greater protection of egg sacs and young, early warning against potential predators and the ability to exploit habitats not available to single individuals (Lubin, 1974; Rypstra, 1979; Uetz, 1989; Uetz and Heiber, 1997; Leborgne et al., 1998; Whitehouse and Lubin, 2005; Fernández Campón, 2007, 2008). Large colonies, however, incur costs of greater visibility of the colony to predators and parasites and increased competition for resources within the colony (Lubin, 1974; Uetz and Heiber, 1997). Comparisons among populations of a single species and among related species suggest that the spatial distribution of prey influences grouping tendency (Lubin, 1980; Uetz et al., 1982), while the potential influence of costs of dispersal on grouping tendency have scarcely been examined (Waser et al., 1994; Jakob et al., 2001).

In this study, we examined the role of ecological constraints on dispersal in determining group living in the colonial spider *Cyrtophora citricola* (Araneae: Araneidae). In the hyper-arid Arava valley of Israel, *C. citricola* colonies are found in clumps of trees in oases and along seasonally dry watercourses. We tested the idea that group living

in these populations and the pattern of colony dispersion result from a combination of ecological constraints on dispersal, on the one hand, and the benefits of natal philopatry, on the other. In particular, we asked whether clustering of groups occurred because of (1) large distances between trees, making colonization of new tree clusters difficult; (2) differences in resource patch quality among trees; or (3) the benefits of natal philopatry. We predicted that (1) unoccupied trees would be further away from occupied trees than the distance between neighboring occupied trees; (2) unoccupied trees would be in poorer condition than occupied trees; and (3) that spiders that arrived at trees containing conspecifics would be more likely to remain and build webs than those arriving at unoccupied trees.

MATERIALS AND METHODS

STUDY SITES

Low-density desert populations of *C. citricola* were recorded at several sites along the Afro-Syrian rift in the Jordan and Arava Valleys in Israel (Levy, 1997). The Arava is an extreme desert habitat with less than 50 mm average annual precipitation and large variance among years. Average daily temperatures range from 16 to 33 °C, with a maximum of 48 °C, and the relative humidity is low (26–55%) (Arava R&D Agriculture Information Center, 1998).

The dominant woody vegetation of the Arava valley consists of *Acacia* trees (*Acacia tortillis* and *A. raddiana*), which occur in dry stream beds (wadis). However, the distribution of these trees is patchy and they are generally found in scattered locations along wadis. Colonies are most commonly found on *Acacia* trees, and to a lesser extent on small shrubs such as *Anabasis* sp. and *Hamada* sp. (Chenopodiaceae). Colonies in trees are situated predominantly on the south-southeast side of the tree (Rao, 2003). We found *C. citricola* in the following sites in the Arava Valley: Shezaf Nature Reserve (30°44'10.92"N, 35°15'33.58"E), Ein Dohan (30°42'46.980"N, 35°11'22.019"E), Ein Yahav (30°39'3"N, 35°13'41"E), and a pump station near Ein Yahav and Moa (30°32'35.82"N, 35°11'25.98"E). The study was done at the Ein Dohan oasis and wadi. For the experiments, spiders and eggsacs were collected from a large colony at Ein Yahav.

STUDY SPECIES

Cyrtophora citricola (Forsskål, 1775) is a colonial spider that has a wide distribution in the Old World and was also introduced into Hispaniola and Colombia (Platnick, 2010) and recently to southeastern USA (C. Mannion, pers. comm.). It occurs in colonies ranging from a few individuals to several hundreds, but it may also build solitary webs (Leborgne et al., 1998). *Cyrtophora citricola* builds a three dimensional web made of a fine-meshed horizontal sheet, a tangle of threads above the sheet and often a retreat made of leaf debris at the hub (Kullmann, 1958; Blanke., 1972; D'Andrea, 1987). The web forms a "knock-down" trap for flying insects (Lubin, 1980). In large colonies, where

individual webs are arranged in layers, the inner webs are more protected from physical damage and predators than the outer webs, but spiders in outer webs receive more prey (Ryptsra, 1979). Layers were not seen in the desert colonies due to the small average size of the colonies (approximately 10 individuals; Rao, 2003). In the Ein Dohan population, colony size ranges from 2 to 50 individuals. Large colonies of more than 100 individuals were seen in only two locations in the Arava: at Ein Yahav, where the colonies were located near a garbage dump, and at the pump station near Ein Yahav.

Adult females live up to a year and they produce an average of 1–3 eggsacs containing 22 eggs (Rao, 2003). Eggsacs are suspended above the hub and the uppermost eggsac is the oldest one. Eggsacs were found throughout the year in the Arava colonies, but there are two peaks in eggsac production, in June and in December (Rao, 2003). After hatching, spiderlings often construct small webs within the framework of the female's web. *Cyrtophora citricola* disperses at the juvenile stage by means of ballooning, bridging, or walking on the substrate (Blanke, 1972).

ECOLOGICAL CONSTRAINTS ON DISPERSAL

We assessed the quality and accessibility of alternative sites in three ways:

1. *Spatial arrangement of trees.* We mapped all the *Acacia* trees at Ein Dohan using a Global Positioning System unit (GARMIN GPS 12XL) and noted which of these trees contained colonies. Distances between a given tree and every other tree were calculated using the Geographical Information System (GIS) software CrimeStat Ver. 2.0 (Levine, 2002).

Nearest neighbor distance was measured for each occupied tree to the nearest occupied tree (O–O) and to the nearest unoccupied tree (O–N). The mean nearest neighbor distance (NND) was calculated using the formula (after Clark and Evans, 1954, cited in Southwood, 1978):

$$\text{NND}(d) = \sum_{(n)}^N \frac{\text{Min}(d_{ij})}{N}$$

where $\text{Min}(d_{ij})$ is the distance (d) between each tree (i) and its nearest neighbor (j) and N is the number of trees. We then tested by simulation whether the difference in mean NND between *occupied* trees (O–O) in the data set was different from that for 1000 trees randomly drawn from the total population of trees. Since there were 18 trees occupied by colonies in the sample, for the random sample 18 trees were chosen randomly at each draw (ensuring that the same tree did not appear more than once in each sample) and distances to the nearest occupied and unoccupied trees were recorded for each. The simulations were performed in Matlab.

An index of clumping was calculated using the method of David and Moore (1954, cited in Southwood, 1978), which compares the mean number of individuals found in the plots to the variance in the number of individuals. For the index, the ratio between the mean and the variance is calculated and 1 is then subtracted from the ratio, with the result that a value of zero indicates a random distribution pattern and a higher

value determines the degree of clumping. We selected a part of the Ein Dohan site, where there were trees with colonies, and divided the selected area arbitrarily into 30 plots of 5 × 5 m area (for a total area of 750 m²) and noted the number of colonies per plot. The index was calculated using the following formula:

$$I_{DM} = \frac{S^2}{\bar{x}} = 1$$

where s^2 is the variance and \bar{x} is the mean number of colonies per plot.

2. *Prey availability.* The potential prey available to spiders on *Acacia* trees was determined by placing insect traps at approximately 2 m height on occupied trees ($n = 10$) and unoccupied trees ($n = 10$) and at ~0.5 m height in unoccupied shrubs ($n = 10$). The insect traps consisted of yellow plastic rectangles (23 × 14 cm) covered on both sides with a thin layer of sticky substance (Rimiput™). Yellow sticky traps are routinely used in studies assessing the abundance of insects. Traps were left in place for 24 h in May and September, 2002, and March, 2003. Flying insects caught on the sticky traps were counted and segregated into two size categories: <5 mm and >5 mm. Since *C. citricola* captures mainly small flying insects (Y. Lubin, pers. obs.), only insects <5 mm were considered in the analysis. Traps were also placed on the north and south sides of occupied trees to determine if there was any difference between the two sides based on insect availability. In order to examine the possibility that the size of the tree could influence the results, we compared the crown areas of occupied and unoccupied trees. Since *Acacia* crowns are roughly elliptical in shape, we measured crown diameter along two axes (long axis and short axis) and approximated the crown area as an ellipse. Differences in crown area were compared with a *t*-test.
3. *Tree condition.* The condition of the tree can indicate the suitability of the site for spiders because a tree with more fruits, flowers, and leaves is likely to attract more prey, and the presence of leaves may provide protection from wind. The abundance of fruits, flowers, and leaves was ranked in occupied ($n = 10$) and randomly selected unoccupied trees ($n = 10$) on a scale of 0 to 5. For example, for flowering, a rank of 0 meant that there were no flowers and a rank of 5 meant that more than 90% of the tree branches had flowers. Similarly, for fruiting, a ranking of 0 meant that there were no fruits and a rank of 5 meant that more than 90% of the tree branches had fruits. For foliage, a ranking of 0 meant that there were no leaves and a rank of 5 meant that more than 90% of the tree branches had leaves. Ranking was done once a month for a period of 10 months (June, 2002, to March, 2003).

COLONY ESTABLISHMENT EXPERIMENTS

We conducted an experiment in semi-captive conditions to test the hypothesis that spiders prefer to settle in existing colonies rather than in unoccupied sites. We measured the time taken by dispersing individuals to establish webs in trees with and without existing colonies. For this experiment we set up 30 potted *Acacia raddiana* trees in an outdoor, screened greenhouse at the Institute for Desert Research in Sede Boqer. The

approximate height of the potted trees was 2 m. The trees were spaced 1 m apart and arranged in three rows of 10 trees each. We established artificial colonies on these potted trees by introducing adult female spiders taken from the Ein Yahav colony. We covered the trees with cotton mesh to make sure that the spiders would construct webs only on the trees. After the webs had been built, we removed the restraining mesh and fed the spiders with *Drosophila* flies *ad libitum* for about five days. Each colony consisted of three to five individuals. We refer to this as the “host colony”. Juveniles (approximately 3 mm total body length) were also collected from the large colony in Ein Yahav. The juveniles were marked with a spot of paint on the dorsal side of the abdomen using a fine brush. Each juvenile was color-coded according to the treatment. One marked juvenile was introduced per tree and the trees were monitored daily to determine the time taken to build a web. We noted whether the introduced spiders had built webs and whether they had built retreats. There were three treatments, spatially arranged in sequence in each row, but in such a way that trees with the same treatment were not next to one another. The treatments were as follows:

1. Trees with host spiders on their webs ($n = 10$).
2. Trees from which the host spiders were removed after the webs had been built, thereby eliminating the influence of the host spider itself ($n = 10$).
3. Control trees without spiders or webs ($n = 10$).

STATISTICAL ANALYSES

All the statistical analyses were done in SYSTAT (Version 10) unless stated otherwise. Data were tested for normality and transformed when necessary.

A repeated measures ANOVA was used to test for differences among the potential prey available in previously identified occupied trees, unoccupied trees, and in unoccupied shrubs ($n = 10$ each), and also on the two sides of the tree. We also tested for the effect of crown area on the abundance of insects between occupied and unoccupied trees using repeated-measures ANOVA with crown area as covariate, number of insects as dependent, and the occupancy of trees by the spiders as the factor.

Logistic regression (binary logit analysis) was used to test for probabilities of occupation of trees ($n = 10$) by spiders in relation to their phenological state, namely, presence and amount of flowers, fruits, and leaves. State of occupancy was the dependent variable, and phenological ranks were the independent variables.

We used survival analysis (Selvin, 1995) to determine whether there were differences between the three treatments, in the time taken to build webs by marked juveniles. For this analysis, the time was taken between the release of the juvenile spiders onto the trees and the construction of a web. Thus, the survival function is defined as 1 minus the cumulative proportion of spiders with webs. A Tarone–Ware log-rank test was used to test for pair-wise differences in the survival curves obtained for the three treatments. We used a χ^2 test of independence to determine if there were differences among the three treatments with respect to the total number of individuals that built webs and retreats.

RESULTS

SPATIAL ARRANGEMENT

Colonies of *C. citricola* at Ein Dohan follow an east–west trajectory, approximately along the wadi bed, which runs slightly NE–SW (Fig. 1). The maximum extent of the colony patch along an E–W axis was 40 m, and along the N–S axis 10 m. Trees with colonies were clumped: the index of clumping (I_{DM}) was 7 (mean \pm S.D. = 0.6 ± 2.2 colonies per quadrat, number of occupied quadrats = 3, total number of colonies = 18).

We tested whether the colonies in Ein Dohan were clustered due to a greater distance to unoccupied trees, such that dispersing spiders might incur a large cost to reach them. The mean NND from one occupied tree to another (O–O) was 3.51 ± 2.89 m and from an occupied tree to its NN unoccupied tree (O–N) was 4.82 ± 1.89 m. The observed difference in NND between an occupied tree and an unoccupied tree was on average -1.31 ± 2.74 m. For the randomly selected trees, NND to the nearest occupied tree was 28.39 ± 5.66 m and to the nearest unoccupied tree 4.38 ± 0.76 m and the average difference was 23.84 ± 5.58 m. Comparing the mean differences in NND to an occupied and unoccupied tree for the observed and expected data sets (-1.31 ± 2.74 m and 23.84 ± 5.58 m, respectively) showed that the NND between occupied trees was significantly smaller than would be expected by chance alone.

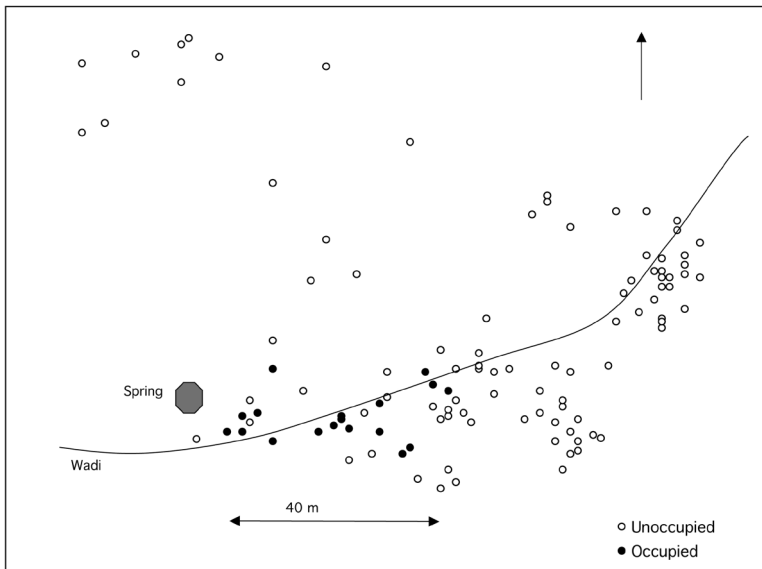


Fig. 1. Map of Ein Dohan, Arava Valley, Israel showing locations of *C. citricola* colonies (occupied *Acacia* trees—filled circles; unoccupied *Acacia* trees—empty circles). Arrow indicates north.

Table 1

Numbers of insects (≤ 5 mm body length) constituting potential prey captured in trees occupied by *C. citricola* colonies, in unoccupied trees and in unoccupied shrubs over the period of the study (n = 10 in each group). Numbers are mean \pm S.D.

Potential Prey	Unoccupied	Occupied	Shrubs
March	223.6 \pm 138.5	175.4 \pm 212.55	173.9 \pm 88.22
May	90.6 \pm 69.63	20.3 \pm 12.63	37.1 \pm 24.03
Sept	72.2 \pm 58.17	70.1 \pm 42.09	66.6 \pm 42.16

Table 2

ANCOVA for the number insects trapped, with tree crown diameter as covariate. There was no effect of tree size as measured by crown diameter on the abundance of insects in occupied and unoccupied trees (n = 10 trees in each group)

Source	SS	df	MS	F	p
Colony	245.4	1	245.4	0.18	0.68
Crown	145.05	1	145.05	0.11	0.75
Colony*Crown	2143.36	1	2143.36	1.59	0.23
Error	21624.8	16	1351.55		

PREY AVAILABILITY

There was no significant difference in prey availability in trees with colonies, trees without colonies, and shrubs without colonies (repeated measures ANOVA, $F_{2,27} = 1.77$, $p = 0.18$) (Table 1), although unoccupied trees had more insects on average than occupied trees or shrubs (mean \pm S.D. number of insects = 64.4 \pm 68.5, 46.2 \pm 50.7 and 44.3 \pm 69.5, respectively). Since the size of the tree could influence the abundance of insects, we tested for differences in crown area. There was no significant difference in crown area between unoccupied trees (mean \pm S.D. = 33.6 \pm 23 m²) and occupied trees (mean \pm S.D. = 18.8 \pm 8.5 m²; $t = 1.916$, $df = 18$, $p = 0.07$), and the crown area did not affect the abundance of insects in occupied and unoccupied trees in the study site (Table 2). Significantly more insects were trapped on the south side of occupied trees (mean \pm S.D. = 92.5 \pm 81.9 prey items) than on the north side (mean \pm S.D. = 63.3 \pm 43.7 prey items; repeated measures ANOVA for aspect, $F_{1,18} = 5.08$, $p = 0.03$).

TREE CONDITION

We compared the abundance of flowers and fruits and the presence of dense foliage, in trees occupied by colonies and in randomly selected unoccupied trees. Mean ranks are given in Table 3. Adjacent trees did not necessarily share similar phenological characteristics; for example in November, 2002, Tree #6 had a rank of 4 for flowering while the adjacent Tree #5 had a rank of 0. There was no difference between occupied trees and unoccupied trees based on average ranks of flowering (log likelihood, $LL = 0.34$, $df = 1$,

Table 3

Mean \pm S.D. of phenological ranks (ranked from 0–5, with 5 being highest) of occupied and unoccupied *Acacia tortillis* (n = 10 each). *p* values are from logistic regressions for each variable

<i>Acacia tortillis</i>	Occupied trees	Unoccupied trees	<i>p</i>
Flowers	2.6 \pm 1.26	2.3 \pm 1.06	0.54
Fruit	2.2 \pm 1.4	2.7 \pm 1.57	0.43
Foliage	3.68 \pm 0.66	3.17 \pm 0.85	0.14

$p = 0.54$), fruiting (LL = 0.62, df = 1, $p = 0.43$), or foliage (LL = 2.17, df = 1, $p = 0.14$) (logistic regression, binary logit analysis, n = 10 each).

COLONY ESTABLISHMENT

Spiders built their webs over a period of one to three days. There were significant differences among the survival curves describing the latency to establish webs in the three treatments (Fig. 2) (log rank test of the overall model, $\chi^2 = 5.83$, df = 2, $p = 0.054$). Pair-wise tests revealed that there was a significant difference in time to establish webs between the control group and the group of host webs with spiders (log rank test, $\chi^2 = 4.33$, df = 1, $p = 0.04$); and between controls and host webs without spiders (log rank test, $\chi^2 = 4.73$, df = 1, $p = 0.03$). There was no significant difference in the rate of web construction when confronted with host webs with spiders and without spiders (log rank

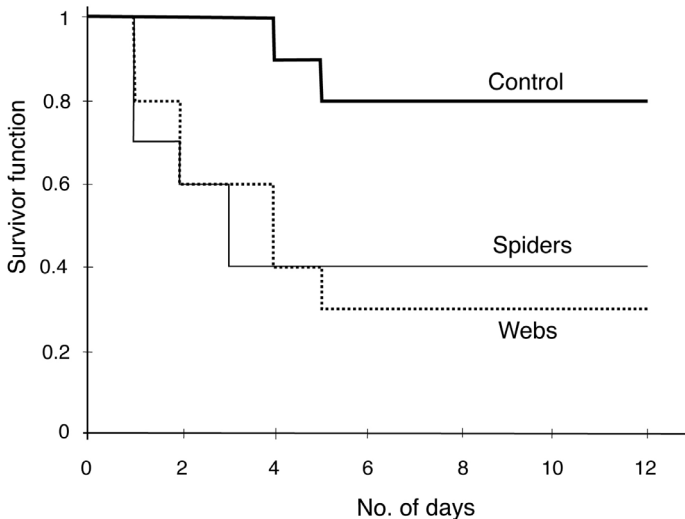


Fig. 2. Survival analysis showing number of days to build webs by juveniles for all treatments: survivor function is one minus the cumulative proportion of individuals that built webs (see text for details).

test, $\chi^2 = 0.014$, $df = 1$, $p = 0.9$). Thus, spiders built faster when placed on trees containing webs of conspecifics with or without spiders. Overall, significantly more individuals built webs in the two treatments with host webs in comparison with the controls ($\chi^2 = 8.9$, $df = 2$, $n = 10$, $p = 0.012$; 7/10 Spiders +Webs, 6/10 Webs only, and 2/10 control). This pattern was also seen in the number of individuals that built retreats ($\chi^2 = 10.6$, $df = 2$, $n = 10$, $p = 0.005$; 7/10 Spiders +Webs, 6/10 Webs only, 1/10 control). Only one individual that left the host tree (of 30 marked spiders) was recovered in an adjacent tree.

DISCUSSION

Colonies of *C. citricola* in the Arava are clustered around oases, which are high productivity patches in a hyper-arid environment. The colonies of Ein Dohan were clumped in distribution, following the east–west path of the wadi, and the distance between a tree occupied by a colony and the nearest occupied tree was significantly smaller than expected by chance. Whether a tree was occupied could not be explained by differences in availability of potential prey (small insects) or in the condition of the trees (abundance of flowers, fruits, and foliage). An experiment conducted in controlled conditions, and removing the risk of predation, showed that juvenile spiders remained and established webs more rapidly when webs of conspecifics were present than when placed on unoccupied trees.

Dispersal is a risky event for young spiders (Turnbull, 1973). An individual that remains in the colony benefits by saving costs of searching for a new site and by lowering the risks of mortality during movement. Additionally, the costs of web building in terms of energy and time (Janetos, 1982) may be reduced by using silk lines of other webs (Jakob, 1991; Jakob et al., 2001). *Cyrtophora citricola* typically takes several days to construct its three-dimensional, silk-rich web, which then lasts for many weeks (Zschokke and Vollrath, 1995). A related species, *C. moluccensis* Doleschall 1857, was found to build an energetically more costly web than that of a typical orb-web spider of comparable size (Lubin, 1973). Our results showed an advantage to philopatry for juveniles: they built webs faster when webs of conspecifics were present. Young of *C. citricola* in our experiment avoided settling in trees that had no conspecific silk, which suggests strong selection favoring philopatry, mediated by an attraction to silk of conspecifics.

The results of this study indicate that, within the immediate area of extant colonies, there seemed to be no advantage to shifting from one tree to another in terms of prey availability or other benefits from trees in different phenological condition. Models of dispersal, such as those proposing a “delayed dispersal threshold” (Koenig and Pitelka, 1992) or the “resource dispersion” model (Blackwell and Bacon, 1993) propose that individuals assess current and expected territory quality, incorporating both costs of dispersal and benefits of remaining in the territory in deciding whether or not to disperse. These models assume an ability of the disperser to sample territories and assess their quality. This ability is likely to be lacking in *C. citricola*, given the costs of relocation and web building. Indeed, the evidence from this study suggests that dispersal should be a less favored strategy. Nevertheless, new colonies do become established, as evidenced

by the distribution of colonies within the Ein Dohan oasis and wadi, and the scattered occurrence of colonies in other oases. This begs the question: when and why do spiders leave to establish new colonies?

We propose here that *C. citricola* has succeeded in invading the Arava region owing to the existence of oases and, more recently, human habitation, both of which provide sites that are richer in prey. All the colonies in Ein Dohan (this study) were small, containing a few dozen individuals at most. The spiders themselves are small relative to individuals in more mesic regions (Leborgne et al., 1998; Rao, 2003), and it is likely that conditions are less favorable than in mesic regions within the distribution of the species.

However, large colonies were seen in a few locations, mainly close to human habitation (Ein Yahav garbage dump and pumping station), indicating that, given a rich food source, colonies can grow to contain hundreds of spiders. In the vicinity of the large Ein Yahav dump colony, we found numerous solitary webs and small clusters of webs on low shrubs surrounding the tree that contained the main colony, suggesting recurrent dispersal events. These solitary individuals were sometimes larger or at a more developed stage than their counterparts in the trees (Rao, D., pers. obs.). At such densities, space may become limiting, particularly as colonies are restricted to the south sides of *Acacia* trees (Rao, 2003), and dispersal may become a more rewarding strategy.

Finally, in the past decade there has been high mortality of *Acacia raddiana* trees in some of the Arava oases (Ward and Rohner, 1997), and it is possible that *C. citricola* colony clusters in these oases are suffering a decline in population size associated with stress conditions in the *Acacia* trees. The Shezaf wadi population, for example, decreased during the years 1998–2003 from four medium-sized colonies, to a scattering of groups of a few individuals, and no new colonies appeared in the area during the study period (Rao, D. pers. obs.).

Owing to the scarcity of occupied host trees, we were unable to augment the sample size of colonies in the study. Thus, we cannot generalize about colony establishment in the range of habitats occupied by *C. citricola*. Restricted dispersal in *C. citricola* in the Arava populations is likely driven by a combination of the costs of dispersal to an unoccupied tree and energetic benefits derived from remaining in the colony. We suggest that dispersal events occur mainly in the most prey-rich sites, or in rare, favorable years with higher rainfall. Thus, colonial living in these desert populations seems a viable strategy only in those habitats where and when the extreme desert conditions are ameliorated.

ACKNOWLEDGEMENTS

We thank the Israel National Parks Authority for permission to conduct research in the Shezaf, Ein Shachak, and Ein Dohan Nature Reserves. We thank D. Saltz and D. Gottlieb for help with statistics and programming, respectively, and two anonymous reviewers for helpful comments. This work was conducted with the financial assistance of the Albert Katz School for Desert Studies. This is publication #673 of the Mitrani Department of Desert Ecology. The experiments conducted comply with the current laws of Israel.

REFERENCES

- Arava R&D Agriculture Information Center. 1998. <http://yair.arava.co.il/climatic/makl.htm> (in Hebrew).
- Blackwell, P., Bacon, P.J. 1993. A critique of the territory inheritance hypothesis. *Anim. Behav.* 46: 821–823.
- Blanke, R. 1972. Field studies on the ecology and ethology of *Cyrtophora citricola* Forskal (Araneidae) in Andalusia. *Forma et Functio* 5: 125–206.
- D'Andrea, M. 1987. Social behaviour in spiders (Arachnida: Araneae). *Ital. J. Zool.* 3: 1–156.
- Emlen, S.T. 1994. Benefits, constraints and the evolution of the family. *Trends. Ecol. Evol.* 9(8): 282–285.
- Fernández Campón, F. 2007. Group foraging in the colonial spider, *Parawixia bistriata* (Araneidae): effect of resource levels and prey size. *Anim. Behav.* 74: 1551–1562.
- Fernández Campón, F. 2008. More sharing when there is less: insights on spider sociality from an orb weaver's perspective. *Anim. Behav.* 75: 1063–1073.
- Jakob, E. 1991. Costs and benefits of group living for pholcid spiderlings: losing food, saving silk. *Anim. Behav.* 41: 711–722.
- Jakob, E.M., Porter, A.H., Uetz, G.W. 2001. Site fidelity and the costs of movement among territories: an example from colonial web-building spiders. *Can. J. Zool.* 79(11): 2094–2100.
- Janetos, A.C. 1982. Foraging tactics of two guilds of web-spinning spiders. *Behav. Ecol. Sociobiol.* 10: 19–27.
- Koenig, W.D., Pitelka, F.A. 1992. The evolution of delayed dispersal in cooperative breeders. *Q. Rev. Biol.* 67(2): 111–150.
- Komdeur, J. 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the Seychelles warbler. *Nature* 358: 493–495.
- Krause, J., Ruxton, G.D. 2002. *Living in groups*. Oxford University Press, Oxford.
- Kullmann, E. 1958. Beobachtung des Netzbaues und Beiträge zur Biologie von *Cyrtophora citricola* Forskal (Araneae, Araneidae) (Zugleich ein Beitrag zur Phylogenie der Radnetzspinnen). *Zoologische Jahrbuch Systematik* 86(3): 181–216.
- Leborgne, R., Cantarella, T., Pasquet, A. 1998. Colonial life versus solitary life in *Cyrtophora citricola* (Araneae: Araneidae). *Insectes Sociaux* 45: 125–134.
- Levine, N. 2002. *CrimeStat II: A spatial statistics program for the analysis of crime incident locations (version 2.0)*. Ned Levine & Associates, Houston, TX, and the National Institute of Justice, Washington, DC.
- Levy, G. 1997. Twelve genera of orb-weaver spiders (Araneae, Araneidae) from Israel. *Isr. J. Zool.* 43: 311–365.
- Lindström, E.R. 1986. Territory inheritance and the evolution of group living in carnivores. *Anim. Behav.* 34: 1540–1549.
- Lubin, Y.D. 1973. Web structure and function: the non-adhesive orb-web of *Cyrtophora moluccensis* (Doleschall) (Araneae: Araneidae). *Forma et Functio* 6: 337–358.
- Lubin, Y.D. 1974. Adaptive advantages and the evolution of colony formation in *Cyrtophora* (Araneae: Araneidae). *Zool. J. Linn. Soc.* 54(4): 321–339.
- Lubin, Y.D. 1980. Population studies of two colonial orb-weaving spiders. *Zool. J. Linn. Soc.* 70(3): 265–287.
- Lubin, Y. 2010. Spiders: Social evolution. In: Breed, M.D, Moore, J., eds. *Encyclopedia of Animal Behavior*, Vol. 3, Academic Press, Oxford, pp. 329–334.
- Platnick, N.I. 2010. *The world spider catalog, version 10*. American Museum of Natural History,

- online at <http://research.amnh.org/entomology/spiders/catalog/index.html>.
- Rao, D. 2003. Dispersion and dispersal in a desert spider: *Cyrtophora citricola*. Master's thesis, Ben Gurion University, Israel.
- Rypstra, A.L. 1979. Foraging flocks of spiders. *Behav. Ecol. Sociobiol.* 5: 291–300.
- Rypstra, A.L. 1986. High prey abundance and a reduction in cannibalism: The first step to sociality in spiders (Arachnida). *J. Arachnol.* 14(2): 193–200.
- Selvin, S. 1995. *Practical biostatistical methods*. Wadsworth Publishing Company, Belmont.
- Southwood, T.R.E. 1978. *Ecological methods with special reference to the study of insect populations*, Chapman and Hall, London.
- Turnbull, A.L. 1973. Ecology of true spiders (Araneomorphae). *Annu. Rev. Ecol. Syst.* 18: 305–348.
- Uetz, G.W., Kane, T.C., Stratton, G.E. 1982. Variation in the social grouping tendency of a communal web-building spider. *Science* 217: 547–549.
- Uetz, G.W. 1989. The 'ricochet effect' and prey capture in colonial spiders. *Oecologia* 81: 154–159.
- Uetz, G.W., Heiber, C.S. 1997. Colonial web-building spiders: balancing the costs and benefits of group living. In Choe, J.C., Crespi, B.J., eds. *The evolution of social behavior in insects and arachnids*. Cambridge University Press, Cambridge, pp. 458–475.
- Ward, D., Rohner, C. 1997. Anthropogenic causes of high mortality and low recruitment in three *Acacia* tree taxa in the Negev desert, Israel. *Biodiversity Conserv.* 6: 877–893.
- Waser, P.M., Creel, S.R., Lucas, J.R. 1994. Death and disappearance: estimating mortality risks associated with philopatry and dispersal. *Behav. Ecol.* 5: 135–141.
- Whitehouse, M.E.A., Lubin, Y. 2005. The functions of societies and the evolution of group living: spider societies as a test case. *Biol. Rev.* 80: 1–15.
- Zschokke, S., Vollrath, F. 1995. Web construction patterns in a range of orb-weaving spiders (Araneae). *Eur. J. Entomol.* 92: 523–541.