

Struc. Bio. 1:621-637; Robertson, H.M., C.R. Preston, R.W. Phillis, D.M. Johnson-Schlitz, W.K. Benz, and W.R. Engels 1988, Genetics 118:461-470; Tautz, D., and C. Pfeifle 1989, Chromosoma 98:81-85; Wang, S., and T. Hazelrigg 1994, Nature 369:400-403.

Breitmeyer, C., and G. Hocutt. Arizona State University, Tempe, AZ 85287. Alternative feeding sites in desert *Drosophila*: fly-ant interactions.

Host plant specificity has long been the cornerstone of our understanding of the basic ecology of the cactophilic *Drosophila* of the Sonoran Desert (Heed, 1978). Sonoran Desert *Drosophila* use specific host cacti necroses as sites for feeding and breeding.

Oviposition and larval development take place within the necrotic tissue while the adults feed on the surface. In the case of one of these species, *D. pachea* (Patterson and Wheeler, 1942), a unique sterol found in the decaying tissue of its host *Lophocereus schottii* (senita), is actually required for successful larval development (Heed and Kircher, 1965).

One assumption made by many investigators is that the necrotic cactus tissue and its microbial flora are the sole nutritional source for the adult flies. However, this necrotic tissue contains many physiologically taxing secondary compounds and, therefore, may not provide an optimum source of nutrition. A source of free sugars, such as those produced by extrafloral nectaries would provide a much richer energy source as well as free amino acids at a lower metabolic cost (Baker *et al.*, 1978). Data on spatial resource availability indicates that rot distribution for these cactophilic species is patchy and for some species suitable substrates are rare (Breitmeyer and Markow, 1998). Sonoran Desert *Drosophila* have the ability to disperse over 2 km in a 24 hour period (Johnston and Heed, 1976; Breitmeyer, unpub.). Flights of this distance would require a significant expenditure of energy. Ganter, Starmer, Lachance and Phaff (1986) hypothesized that non-cactus food sources may be used by dispersing flies. Until now there have been no previous reports of cactophilic *Drosophila* utilizing alternative feeding sites. Here we present observational data indicating that alternative food sources are available to, and are utilized by, at least some of these cactophilic *Drosophila* species.

We observed flies of two species, *D. pachea* and *D. arizonae* (Ruiz, Heed and Wasserman, 1990), feeding at the extra floral nectaries of senita cacti during two separate periods in October 1995 and May 1996 near San Carlos, Sonora, Mexico. Observations were made at each cactus for approximately 10 minutes. Flies were concentrated on the terminal end of a single cactus arm in groups of 5-10 individuals, and these clusters were always associated with a necrosis found on another arm of the same cactus. The observations of *D. arizonae* occurred where its preferred host, *Stenocereus alamosensis*, is absent from the local area. *Drosophila arizonae* is the sister species of the Sonoran desert endemic *D. mojavensis*, both of which are considered generalists. Observed along with the feeding *Drosophila* were large ants of the Genus *Pseudomyrmex*. Ants in this genus have been reported to have an association with both barrel and prickly pear cactus nectaries (Pickett and Clark, 1979; Ruffner and Clark, 1986). These ants associated with the extrafloral nectaries of senita were observed to prey upon the *Drosophila* and appeared to be tending the extra-floral nectaries, perhaps feeding on them or promoting nectar flow to bait in more *Drosophila* prey. This behavior is an ant actively chasing a fly found near the nectaries.

With the exception of one cactus, *D. arizonae* were more numerous than *D. pachea* (Table 1). While these numbers are not large they are comparable to the numbers of *D. pachea* aspirated from cactus rots during the same time period. Population sizes of *D. pachea* have been estimated by mark-recapture to be as low as 15-20 individuals (Breitmeyer and Markow, 1998). The individuals observed feeding at the nectaries may account for 5-20 percent of the *D. pachea* population at a given plant. Additional *Drosophila* have been observed feeding at the nectaries since the initial discovery, but their numbers have not been quantified. When flies were observed at nectaries they were never more than 30 cm away, unless being pursued by an ant. The *Drosophila* did not resort to aerial escape immediately and pursuits lasted 15-30 seconds.

Ant behavior was distributed evenly over the three categories (Table 2). Table 2 does not reflect the amount of time spent in each activity. Although no direct measurements of time spent in each behavior were made, approximately 90 percent of ant behavior was split between tending and guarding with short bouts of pursuit. The presence of a fly near the nectary did not always illicit a pursuit response. A few *Drosophila* were able to feed successfully and escape unmolested. Two ants were observed with flies in their mouthparts and were scored as pursuing.

Discussion: Because of its ability to detoxify Senita sterols and its unique dependence on one of them for development, *D. pachea* is considered the extreme specialist of the four Sonoran desert endemic *Drosophila*. These data represent the first confirmed use of an alternative feeding site for *D. pachea*, demonstrating that at least one species of cactophilic *Drosophila* is not strictly dependent on the host plant for all its nutritional requirements. The absence of the preferred host of *D. arizonae* from the local area of our observations indicates that this species may use extrafloral nectaries during dispersal. It is reasonable to expect that *D. mojavensis*, the sister species, has these same resources

Table 1. Observations of *Drosophila pachea* and *Drosophila arizonae* feeding at the terminal extrafloral nectaries of six senita cacti.

Senita #	<i>D. pachea</i>	<i>D. arizonae</i>
1	4	2
2	2	7
3	4	6
4	1	5
5	2	3
6	2	3

Table 2. Number of ants observed and their primary behaviors at extrafloral nectaries of senita cacti. Individual ants were classified as tending or guarding based upon the amount of time spent engaging in this activity, although they may have engaged in both behaviors.

Senita #	Number of Ants	Tending	Guarding	Number of Pursuits
1	2	2	0	0
2	1	1	0	2
3	2	0	2	0
4	2	0	2	2
5	1	1	0	1
6	2	1	1	0

available to it during dispersal. In addition, pollenia have been observed in the mouthparts of *D. nigrospiracula* (Polak and Markow 1998). Members of our lab have observed what appears to be juice from saguaro and/or *Opuntia* fruit in the abdomens of *D. mojavensis*, *D. nigrospiracula*, and *D. mettleri*. These findings raise questions regarding our knowledge of the basic ecology of the Sonoran Desert *Drosophila*. Breitmeyer and Markow (1998) demonstrated that there is an annual lack of utilization of host plants by flies in August. One hypothesis, suggested by the observations reported here, is that the *Drosophila* are able to utilize alternative food sources and, thus, survive whatever conditions make the host plants unsuitable during the summer months. It should be noted that the observation of these flies at the nectaries occurred during a period when there were less than the usual number of rots available. Perhaps, these flies are not consistently observed feeding at the nectaries at other times due to a high risk of predation. During periods when resources are depleted *Drosophila pachea* may be forced to feed at these alternative sites.

These findings also have implications for dispersal in these flies. The ability to use alternative food sources would greatly enhance the chances of these flies to survive long enough to locate suitable necroses for mating and oviposition. The other cactophilic *Drosophila* endemic to the Sonoran Desert often face large distances separating suitable hosts. Understanding the role that alternative hosts play in aiding dispersal will allow us to answer questions about gene flow in all four of these species. In addition, the use of alternative feeding sites may be one explanation for the apparent disappearance of these flies from July through early October. Our findings do not challenge the concept of host cactus specificity but rather the degree of dependence of each *Drosophila* species on actual necroses for their nutritional requirements. Further investigation into the feeding behavior and physiology of all of the Sonoran Desert *Drosophila* should be pursued. In addition, these cactus-fly-ant interactions merit further investigation.

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References: Baker, H.G., P.A. Opler, and I. Baker 1978, *Botanical Gazette* 139: 322-332; Breitmeyer, C., and T.A. Markow 1998, *Functional Ecology* 12: 14-21; Carrol, C.R., and D.H. Janzen 1973, *Ann. Rev. of Ecol. and Syst.* 4: 231-257; Ganter, P.F., W.T. Starmer, M.A. Lachance, and H.J. Phaff 1986, *Oecologia* 70: 386-392; Heed, W.B., 1978, *Ecology and Genetics of Sonoran Desert Drosophila. Proceeding in the Life Sciences, Ecological Genetics: the Interface* (ed P.F. Brussard), pp.109-126. Springer, New York; Heed, W.B., and H.W. Kircher 1965, *Science* 149: 758-761; Johnston, J.S., and W.B. Heed 1976, *The American Naturalist* 110: 629-651; Patterson, J.T., and M.R. Wheeler 1942, *University of Texas Press* 4213: 67-109; Pickett, C.H., and D.W. Clark 1979, *American J. Botany* 66: 618-625; Polak, M., and T.A. Markow 1998, A note on the feeding ecology of *Drosophila nigrospiracula* a Sonoran Desert endemic fruitfly. *Drosophila Information Service*, in press; Ruffner, C.A., and D.W. Clark 1986, *American J. Botany* 73: 185-189; Ruiz, A., W.B. Heed, and M. Wasserman 1990, *J. Heredity* 81: 30-42.