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Resource availability and population size in cactophilic *Drosophila*

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Summary

1. Four species of *Drosophila*, *Drosophila nigrospiracula* (Patterson & Wheeler 1942), *Drosophila mettleri* (Heed 1977), *Drosophila pachea* (Patterson & Wheeler 1942), and *Drosophila mojavensis* (Patterson & Crow 1940), are endemic to the Sonoran Desert of North America and breed in different species of necrotic columnar cacti. Differences in resource availability have been suggested to explain the inter-specific variability in fly population biology, but resource availability for these species has not been quantitatively assessed thoroughly in either spatial or temporal terms. The resource availability was quantified quarterly at three sites for 3 years and population sizes for each *Drosophila* species were estimated.
2. Spatial and temporal availability of resources differed significantly among species of host cacti, with organpipe cactus (*Stenocereus thurberi*) being the least abundant and senita (*Lophocereus schottii*) the most abundant spatially.
3. *Drosophila* species differed significantly in population size. The largest population sizes were found for *D. nigrospiracula* and *D. mojavensis* and smallest for *D. pachea*. Populations of *D. mettleri* were intermediate to these.
4. Population size was greatest for fly species utilizing host species having the largest and longest lasting necroses.
5. Resource availability does not explain the reduction of fly populations in the summer. Necroses were most abundant when flies were absent.

Key-words: Ecology, fruit flies, necrotic cacti, Sonoran desert

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Introduction

Temporal and spatial aspects of resource availability are considered to have important consequences for population biology. At the genetic level, resource availability can impact the structure and evolutionary potential of the population. For example, small isolated populations should be prone to genetic drift or to cycles of extinction and recolonization, and to a large extent a population's size depends upon the size, persistence, and distribution of its resources, but present knowledge of the ecology of metapopulations remains quite limited (McCauley 1991, 1993; Thompson 1996). Life-history variation, especially allocation to reproduction, also has been linked to resource availability, where the need to forage extensively influences the energy available for reproduction (Boggs 1992).

One group of organisms with the potential to address the relationship between resource availability and population biology is those species of *Drosophila* that breed in necrotic cacti. Although a large number

of *Drosophila* species utilize cactus necroses, or rots, four are endemic to the Sonoran Desert of North America and are the core of the cactus–microorganism–*Drosophila* model system (Barker & Starmer 1982). Of these four, one, *D. pachea*, belongs to the nannoptera species group, while the other three are in unrelated subgroups of the repleta species group (Heed 1982). Each *Drosophila* species has an essentially exclusive relationship with a particular species of columnar cactus within any geographic locality (Heed 1978). These are summarized in Table 1 for populations of these species living in Arizona and Sonora and reflect the relationships between the flies, the unique chemical profiles of their hosts and the microorganisms involved in the necrotic succession (Barker & Starmer 1982).

Similar processes initiate necrosis formation in all species of cactus hosts. Once a cactus is injured, colonization by bacteria and yeasts creates a 'rot pocket' that serves as a feeding and breeding site for *Drosophila*. Fermentation produces volatiles that are different for each host cactus and serve to attract adult *Drosophila* for feeding and mating. Adults mate on the surface of the cactus or inside of the rot pocket,

depending upon the species, and females oviposit in the cactus tissue. Larval development is completed in the necrotic tissue or in the soil soaked with liquid from a necrotic cactus. The timing of the dispersal of eclosing adults is unknown.

Well-defined phylogenies and host associations, coupled with the ease of laboratory rearing, have made this group of *Drosophila* an important focus for evolutionary studies. Certain features of their ecology are more clearly defined than for any other *Drosophila* species. The majority of the studies on the ecological relationships between cacti and their flies deal with the adaptations of flies to the chemical properties of their hosts (Fogleman & Abril 1990). However, spatial and temporal availability, those resource characteristics with the greatest potential to influence genetic differentiation and life history evolution, are the least well known. Preliminary data reported by Mangan (1982) suggest the existence of significant differences among hosts in spatial and temporal distribution of necroses, but are too limited to allow generalizations.

Also unknown is the typical size of populations of the four desert *Drosophila* species. Discrete and sometimes large populations of flies aggregate at necrotic hosts, but no comparative estimates are available of population size for the four species. Collection records indicate that all four species of *Drosophila* undergo substantial contractions in population size in July, August and September, when few investigators have found flies, despite exhaustive searches. Rockwood-Sluss, Johnston & Heed (1973) reported collecting 141 adult *D. pachea* in July 1970 and five adults in August 1971 near Santa Ana, Sonora. A collection in August, 1991 near San Carlos, Sonora, yielded nine adult *D. pachea* (Pitnick 1993). Sluss (1975) collected 42 *D. nigrospiracula* near Altar, Sonora, in August 1971. For *D. mojavensis*, collections in 1965 yielded 165 flies in July near Oputo, Sonora, and 20 more in August near Caborca, Sonora (Fellows & Heed 1972). Collections at other times of the year typically yield several hundred to several thousand flies with considerably less effort (Sluss 1975; Johnston & Heed 1975, 1976; Ruiz & Heed 1988).

An explanation for the apparent reduction in fly populations is suggested by the observation of Mangan (1982) of a substantial drop in the number of necroses for all host cacti from February to May. A

continuation of this decline, if typical of annual changes, could explain the observed near-disappearance of flies in the summer, but unfortunately, those surveys were conducted only in 1 year and were not continued after May.

The first step in unravelling the relationship between resource availability and interspecific variation in fly population biology is the simultaneous assessment of the characteristics of the necroses for each cactus host and of the typical population sizes of each *Drosophila* species. Thus in the present study quarterly surveys were conducted of the distribution of necroses of each host plant at sites in Arizona and Sonora for three consecutive years. Using capture-mark-recapture, the sizes of the *Drosophila* populations typically aggregated at each host cactus were also estimated. These data were used to examine the hypothesis that resource availability influences population biology of cactophilic *Drosophila* by testing the following predictions: 1, hosts differ in spatial and temporal aspects of resource availability; 2, the summer decline in fly numbers is explained by an extreme reduction in necrosis number; 3, *Drosophila* species differ in population size; and 4, fly population size is associated with resource availability, such that larger populations are found at the most abundant resources.

Methods

STUDY AREAS

Three sites were selected at which to carry out the study (Fig. 1). Two of the sites were located in the Mexican state of Sonora near the city of Guaymas. One, the San Carlos site, is located at 27°58'N latitude and 111°05'W longitude. The other Mexican site is located at 28°00'W latitude 110°50'N longitude, designated the Guaymas site. These two sites are approximately 23 km apart. The third site was located near the Superstition Mountains east of Tempe, Arizona, at 33°22'N latitude and 111°22'W longitude and is referred to as the Superstition site. At each site, a 15 ha plot was measured and its perimeter staked.

HOST PLANT SURVEYS

Surveys were conducted at quarterly intervals (August, November, February, May) beginning in August 1993, for 3 years. These months were selected for three reasons. First, early February and early August represent dates with very low and high temperatures, respectively. Second, three of the months match those of a previous study at a different location (Mangan 1982) in which the utilization of cacti by flies was reported. Finally, rot availability in August, when flies of all four species are rare, has never been characterized.

During the initial survey period, the cacti on each 15 ha site were mapped utilizing a compass and a range finder according to standard techniques

Table 1. The host plant associations of the cactophilic *Drosophila* found at the three sites in this study

<i>Drosophila</i> species	Host species	Common name
<i>D. mojavensis</i>	<i>Stenocereus thurberi</i>	Organpipe
<i>D. nigrospiracula</i>	<i>Pachycereus pringlei</i>	Cardon
	<i>Carnegiea gigantea</i>	Saguaro
<i>D. pachea</i>	<i>Lophocereus schottii</i>	Senita
<i>D. mettleri</i>	Soaked soil of above hosts	

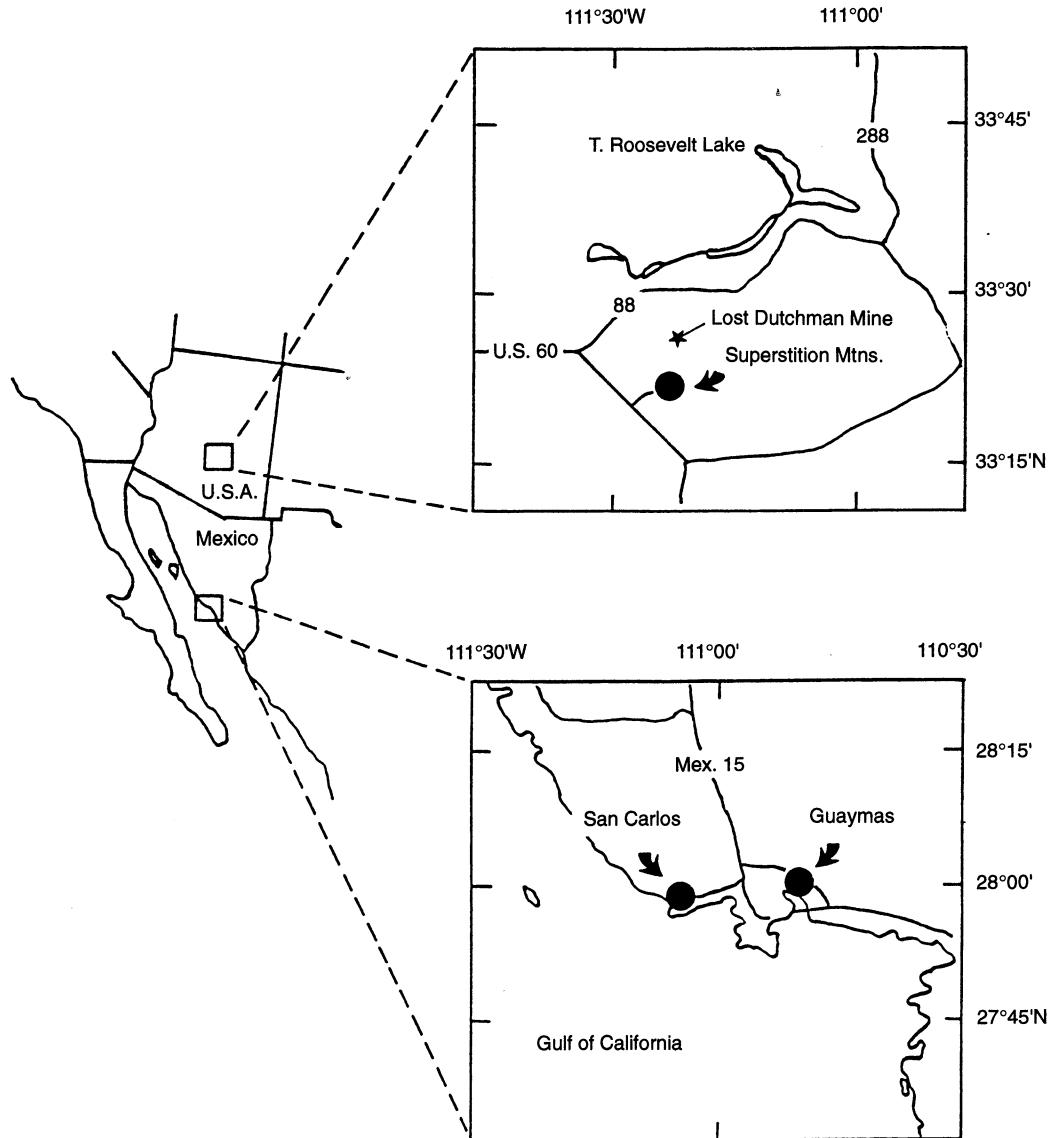


Fig. 1. Locations of the three 15 hectare study sites in Arizona and Sonora.

(Williams 1987). Each cactus was marked with a numbered metal tag and the number of arms on each plant was counted. A subset of plants was measured for arm circumference. Plants were checked rigorously for any necroses, and when one was found, the cactus was marked with a colored flag. Necrosis size, in cm^3 , was estimated on a subset of plants from measures of necrosis length, width and depth. The presence or absence of adult flies was recorded, and from necroses with no flies, about 100 g of substrate was removed and examined for larval forms to verify the absence of *Drosophila*. Those host plants with adult flies were marked with an additional colored flag and utilized in population size estimates.

made in August owing to a lack of flies. Population sizes were estimated using standard mark-recapture techniques. Flies were captured in the mornings before temperatures began to rise. Every effort was made to collect all adult *Drosophila* from a given necrosis, collecting continued until no flies could be located in the immediate vicinity of the rot. Captured flies were marked with a small amount of fluorescent dust (Radiant Co., Richmond, CA) and placed into half pint bottles. Flies from each necrosis were marked with a different color dust. Individuals were counted and allowed ample time to clean themselves of excess dust before release. Bottles were then placed next to the necrotic cactus from where the flies had been caught; flies were released by gently removing the bottle tops to minimize disturbance. The following morning, all flies at the rot were captured, counted and checked for colored dusts. Population size estimates were then generated using the Lincoln-Kennedy

index with Bailey's correction for small sample size (Blower, Cook & Bishop 1981). One assumption of this method is that during the course of the estimate, there is negligible immigration and emigration from the populations being censused. The authors' unpublished data indicate a low rate of movement between necrotic cacti: less than 1% for *D. nigrospiracula*, *D. mojavenensis*, and *D. mettleri* and about 2% for *D. pachea*. Therefore it is assumed that the populations are stable during the course of the census.

Results

RESOURCE AVAILABILITY

Figure 2 illustrates the relative sizes of the four host plants studied and the sizes of their necroses. With the exception of cardon and saguaro, there is little overlap between cactus species in arm circumference. Results from a one way ANOVA were highly significant ($F = 25.24$, $df = 3,58$, $P < 0.0001$). Necrosis size is much more variable, although the rankings are the same. A one way ANOVA for necrosis size was highly significant ($F = 244.32$, $df = 3,53$, $P < 0.0001$), with all of the cactus species, with the exception of cardon and saguaro being significantly different in a Tukey-Kramer Multiple Comparisons test.

Sites differed in composition of cactus species (Table 2). The San Carlos site contained two of the host plants, organpipe and senita. Three host plants, cardon, organpipe, and senita were all found at the Guaymas site. Saguaro was the only host cactus found at the Superstition site. Thus for each fly species, there

were two sites at which the host plant was available. This was true for *D. mettleri* as well, since cardon and saguaro are the most likely cactus species to accumulate enough soaked soil to support larval development.

Table 2 summarizes the host characteristics at each of the sites. While the density and size of the host plants vary by site, these do not affect the number of necroses at a given site. Rot number was not normally distributed and thus was subject to log transformation prior to statistical analysis. Rankings of rot numbers by species were homogeneous between the years, allowing years to be pooled. The results of an ANOVA (Table 3) indicated that the species differed significantly with respect to rot number but that this was not influenced by site. Results of a Duncan's multiple range test ($\alpha = 0.05$) placed senita in a different subset than the other host plants.

Temporal variability in cactus necroses is of two types. One is their incidence at different times of the year and the other is the longevity of a necrosis once it begins. The seasonal frequencies of necroses in the different hosts is shown in Table 4. Because site differences were found to be nonsignificant in the ANOVA, values for Guaymas and San Carlos were pooled for senita and for organpipe. Rot incidence varies among seasons for all cacti, being lowest in May. A one-way ANOVA revealed significant seasonal differences, however, only for senita ($F = 4.33$, $df = 11$, $P < 0.05$). The lack of statistical significance for the other three cacti may reflect the extremely low incidence of necroses in these species at all survey periods.

The other component of temporal variation in rot availability is necrosis duration. While the design of

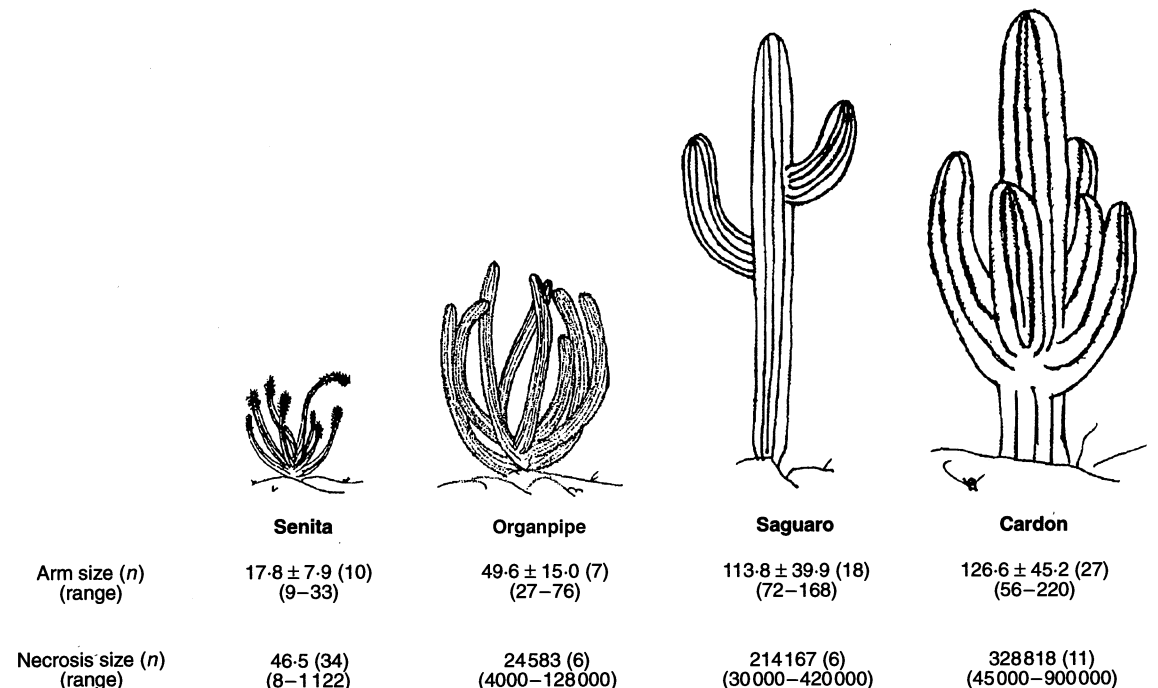


Fig. 2. Average sizes (± SE) of host plants and median sizes of their necroses. Host plant size is based upon arm circumference in cm. Necrosis size was calculated from measures of length, width and depth and are reported in cm³.

this study was not intended to measure rot longevity, host species differences were apparent from the numbers of rots lasting through more than one survey period. The average longevities, based upon survey data, for cardon, saguaro, organpipe, and senita were 8, 6, 4.5, and less than 3 months, respectively. Pools of soaked soil associated with cardon and saguaro were often present at 3 months, but rarely at 6 months after the original recording. However, it is likely that around the base of a rotting cardon or saguaro, the specific location of the soaked soil changes frequently, making 3 months an overestimate. Necrosis duration is clearly associated with plant size and necrosis size (Fig. 2): senita cacti have the thinnest

arms and the smallest necroses, the largest plants are cardon and saguaro, where rots are typically enormous and may last for many months.

Not all necroses are colonized by *Drosophila*. Cardon and saguaro had the highest rates of utilization at 50% or greater. But the use of necroses was not constant across times of the year, either. In May, the colonization of all the cactus species was lower than November and February, and by August, it was effectively zero. The physical appearance of necroses found in August was similar to those observed to have flies at other survey periods. Revisiting these rots at various times of the day still failed to turn up flies and no immature forms were found in the August samples of cactus tissues.

Table 2. Characteristics of host plants at three different 15 hectare sites: average number per hectare (+SE), arms per cactus (\pm SE), rots per survey (+SE), and rots per hectare (\pm SE). Necrosis means are based on 12 survey periods. Designations of NP represent the absence of a particular host at a site

Cactus Species		Study site		
		Guaymas	San Carlos	Superstition
Senita	number (n/ha)	96 (6.4)	137 (9.1)	
	arms/cactus	96.6 \pm 20.5	76.5 \pm 12.0	NP
	rots/survey	29.2 \pm 2.3	25.9 \pm 2.5	
	rots/hectare	1.9 \pm 0.4	1.7 \pm 0.4	
Organpipe	number (n/ha)	137 (9.1)	107 (7.1)	
	arms/cactus	17.4 \pm 3.6	28.3 \pm 1.2	NP
	rots/survey	1.3 \pm 0.9	2.0 \pm 1.2	
	rots/hectare	0.1 \pm 0.0	0.1 \pm 0.0	
Cardon	number (n/ha)	277 (18.4)		
	arms/cactus	14.0 \pm 0.7	NP	NP
	rots/survey	6.3 \pm 1.3		
	rots/hectare	0.4 \pm 0.1		
Saguaro	number (n/ha)			196 (13.0)
	arms/cactus	NP	NP	2.1 \pm 0.1
	rots/survey			1.7 \pm 1.2
	rots/hectare			0.1 \pm 0.0

Table 3. Analysis of variance for log-transformed necrosis number

Source	DF	SS	F Value	P Value
Species	3	12 301.4027	59.75	0.0001
Site	1	28.5208	0.42	0.5216
Month	4	549.3395	2.00	0.1058
Year	3	498.4359	2.42	0.0747
Error	60	4117.4121		

Table 4. Abundance of total necroses, by survey month, and the percentage, in parentheses, of those necroses utilized by *Drosophila* over the three years of the survey

Cactus	Survey month			
	November	February	May	August
Senita	204 (34%)	174 (31%)	102 (17%)	179 (0%)
Organpipe	11 (36%)	11 (36%)	5 (0%)	14 (0%)
Cardon	18 (50%)	22 (55%)	7 (43%)	28 (0%)
Saguaro	6 (50%)	5 (50%)	2 (50%)	3 (0%)

CENSUS OF *DROSOPHILA* POPULATIONS

Table 5 shows the variation in population size present within and among the four Sonoran Desert endemic fly species. Population sizes were zero for all species in August. For the three remaining periods when flies were present, an ANOVA on log-transformed values revealed no significant effect of season on population size in any species (Table 6). Species were significantly different in population size ($P < 0.0001$). The Duncan grouping ($\alpha = 0.05$) yields three size classes. *Drosophila nigrospiracula* and *D. mojavensis* populations were similar in average size. *Drosophila mettleri*, averaging 1000, and *D. packia*, averaging 400 individuals, were in separate size classes. Pairwise comparisons showed the *D. packia* populations at San Carlos to be significantly smaller than those found at Guaymas ($t = 3.26$, $df = 13$, $P = 0.006$), and *D. nigrospiracula* at the Superstition site to have larger populations than at Guaymas ($t = 2.51$, $df = 15$, $P = 0.024$).

Discussion

The first prediction, that host cacti differ in spatial and temporal necrosis availability, was confirmed. There are two kinds of spatial availability, for cactus necroses. The first is the number of necroses or patches per hectare, the second is size of the patches, independent of their density in an area. On the basis of density, rots per hectare, the rank order of the host cacti is senita > cardon > organpipe = saguaro. But the host cactus species differ significantly in necrosis size, such that a ranking inverse to that of density, cardon > saguaro > organpipe > senita, is found. Thus on the basis of the number of patches per hectare, senita is the most abundant, but on the basis of necrosis biomass per hectare it is the least abundant. Saguaro, organpipe and cardon necroses are large, but are less frequently encountered. The difference between the two rankings reflects two extremes: the small but frequent senita rots vs the large but infrequent cardon rots.

Temporal variability in resource availability also has two components. One is the length of time a given necrosis or soaked soil patch persists. Second is the availability during different seasons of the year. Clearly, patch size is related to duration; the longest lasting necroses are found in the species with the largest necroses, cardon. Senita rots and soaked soil persist for the shortest amounts of time. On a seasonal basis, rots are least abundant in the spring and most abundant in the summer. This difference is quite striking for senita, where large numbers of necroses account for the ability to detect statistically significant seasonal differences in availability.

In summary, there are small, more ephemeral necroses that occur at high density, as observed for senita, and large stable necroses, exemplified by cardon, saguaro, or organpipe that are farther apart. There is a reduction both in rot number and rot utilization in the spring. However, this is followed by a high rot number in August, contrary to the prediction based upon the difficulties of finding flies in summer.

The third prediction, that population size would differ among *Drosophila* species, was supported. For this study, a population was operationally defined as the number of individuals found at a specific necrosis. While a population may be defined in a variety of ways, this definition was employed to be consistent with an earlier study of *D. nigrospiracula* (Johnston & Heed 1976) and because the interest was in determining the relationship between resource availability and population size. The last prediction, that population size is related to resource abundance, is true when resource abundance is defined in terms of patch size and duration. The largest population sizes were found in *D. nigrospiracula* whose host necroses are the largest and longest lasting. Because *D. mettleri* adults have occasionally been collected feeding at senita and organpipe as well as on their primary hosts, saguaro

and cardon, adults may experience slightly greater resource availability than predicted on the basis of soil patches alone.

It is possible, using the population size estimates for individual necroses and the density of resources, to calculate the number of flies expected in a neighborhood, defined as a 15 ha study site. These sizes will vary according to season. In August, the size is zero. For seasons in which there are flies, the ranges are 5123–61 476 for *D. nigrospiracula*, 1198–9584 for *D. mettleri*, 9352–16 056 for *D. mojavensis*, and for *D. pachea*, 3192–12 369. Thus the smallest local populations may be those of *D. mettleri* rather than of *D. pachea*, whose individual populations are small, but more abundant because of high resource density.

A number of studies have estimated population size for other *Drosophila* species (Crumpacker & Williams 1973; Shorrocks 1975; Begon 1976; Fontdevilla & Carson 1978; Barker, East & Christiansen 1989). Most of the studies employed baiting, however, a technique that can significantly impact dispersal and numbers of adults (Johnston & Heed 1975), precluding meaningful comparison of results between studies. In the only report of population size for a Sonoran Desert *Drosophila* species, Johnston & Heed (1976), employing the same techniques, estimated the sizes of *D. nigrospiracula* populations at four different cacti to be between 343 and 14 724 per cactus, similar to the authors' own observations. For the non-desert *Drosophila mercatorum* breeding in prickly pear cacti on Hawaii, population size estimates ranged from 8 to 192 flies per cactus (Johnston & Templeton 1982). That study did not include surveys of resource availability, but prickly pear cacti and their necroses appear most similar to senita, with frequent but smaller shorter-lived necroses, and smaller populations of flies.

The relationship between resource availability and population size breaks down completely in the summer. Rot availability is high in August when flies of all species are rare, suggesting that factors in addition to necrosis abundance control populations during this time of the year. Several potential explanations can be invoked to explain this apparent summer bottleneck. Flies may not be able to exist at the high summer temperatures. This can be tested indirectly by long-term studies comparing mild to extreme summers, and directly tested through laboratory thermotolerance experiments. On the other hand, the decrease in rot utilization earlier in the spring may foreshadow the decrease in fly numbers and by the time necroses increase again, populations have become so small that they escape detection. Summer necroses, while abundant, may not be attractive to (Fogleman & Abril 1990) or suitable for *Drosophila*. Even at other times of the year, not all necroses are colonized. And finally, there may not be a bottleneck in summer. Adults may move to a yet undiscovered microhabitat or higher elevation during the summer.

Table 5. Average population size estimates (\pm SE) for each *Drosophila* species. Population sizes reflect number of individuals at a single necrosis

<i>Drosophila</i> Species	Average Size	Range	<i>n</i>
<i>D. nigrospiracula</i>	5123 \pm 1713	260–27 742	18
<i>D. mettleri</i>	1198 \pm 235	30–6554	13
<i>D. pachea</i>	399 \pm 238	16–1690	15
<i>D. mojavensis</i>	5352 \pm 1923	1408–11 500	3

Table 6. Analysis of variance for log-transformed population sizes

Source	DF	SS	<i>F</i> Value	<i>P</i> Value
Species	3	74.0501	14.02	0.0001
Month	2	5.6072	1.59	0.2167
Species X Site	6	3.1150	0.29	0.9356
Error	38	66.9072		

Variation in population biological characteristics such as genetic differentiation and life history evolution of the four *Drosophila* species can now be evaluated in the context of their resource ecology. In order for local differentiation to occur, gene flow must be sufficiently restricted. Comparative dispersal abilities of the four species are unknown. The patterns of resource distribution, however, make strong predictions about dispersal. The low incidence of cardon, saguaro, and organpipe necroses compared to senita, suggests that *D. nigrospiracula*, *D. mettleri*, and *D. mojavensis* should be stronger dispersers than *D. pachea*. If this is the case, evidence of greater local genetic differentiation in *D. pachea* than in the other three species would also be expected.

With the exception of *D. mojavensis* (Zouros 1973), none of the four desert endemic species has been studied in detail at the population genetic level. Preliminary observations suggest, that while genetic variability appears to be comparatively low in desert *Drosophila* (Johnston & Heed 1976), the species show different degrees of local differentiation. Populations of *D. nigrospiracula* and of *D. mojavensis* do not appear to show any genetic subdivision across Arizona and Sonora (Zouros 1973; Sluss 1975), while Rockwood-Sluss *et al.* (1973) and Ward *et al.* (1975) report some geographic differentiation in *D. pachea*, as is expected. All of these observations, however, must be regarded as preliminary. For *D. nigrospiracula* and *D. pachea*, only two and four loci, respectively, have been examined (Sluss 1975; Rockwood-Sluss *et al.* 1973) and for *D. mettleri* no surveys of genetic variation have been published. More complete genetic studies should be undertaken to assess the robustness of the association between population size and structure and genetic differentiation.

The observed spatial and temporal differences in resource availability should affect larvae and adults in different ways (Heed & Mangan 1986). For larvae, a predictable host is one allowing adequate time to complete development. For adults, a predictable host is one that occurs frequently. A large stable necrosis should allow for longer development time and probably larger body size. As predicted above, a host that is infrequently encountered requires greater dispersal capabilities than do hosts that are spatially abundant. Dispersal ability is related to body size in Dipterans (Roff 1977) and Heed & Mangan (1986) suggest that the larval substrate stability experienced by *D. nigrospiracula* underlies its large size and preadapts it to the greater dispersal demands of its host. This suggestion can be tested through comparative studies that control for phylogeny, as well as by comparison of size, dispersal ability, and necrosis distribution for populations living in Baja, where three of the species shift to host cacti that, based upon preliminary observations, differ considerably in resource abundance. Finally, another trait, desiccation resistance, given the arid environment of these flies, is also predicted to be a function of distance between

necroses: those species having to disperse the farthest should be the most resistant to desiccation. These predicted associations currently are under investigation in the authors' laboratory.

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References

- Barker, J.S.F., East, P.D. & Christiansen, F.B. (1989) Estimation of migration from a perturbation experiment in natural populations of *Drosophila buzzatii* Patterson & Wheeler. *Biological Journal of the Linnean Society* **37**, 311-334.
- Barker, J.S.F. & Starmer, W.T. (1982) *Ecological Genetics and Evolution: the Cactus-Yeast-Drosophila Model System*. Academic Press, Sydney.
- Begon, M. (1976) Dispersal, density and microdistribution in *Drosophila subobscura* Collin. *Journal of Animal Ecology* **45**, 411-456.
- Blower, T.G., Cook, L.M. & Bishop, J.R. (1981) *Estimating the Size of Animal Populations*. George Allen & Unwin Ltd, London.
- Boggs, C.L. (1992) Resource allocation: exploring connections between foraging and life history. *Functional Ecology* **6**, 508-518.
- Crumpacker, D.W. & Williams, J.S. (1973) Density, dispersion, and population structure in *Drosophila pseudoobscura*. *Ecological Monographs* **43**, 499-538.
- Fellows, D.P. & Heed, W.B. (1972) Factors affecting host plant selection in desert-adapted *Drosophila*. *Ecology* **53**, 850-858.
- Fogleman, J.C. & Abril, J.R. (1990) Ecological and evolutionary importance of host plant chemistry. *Ecological and Evolutionary Genetics of Drosophila* (eds J. S. F. Barker, W. T. Starmer & R. J. MacIntyre), pp. 121-144. Plenum Press, New York.
- Fontdevilla, A. & Carson, H.L. (1978) Spatial distribution and dispersal in a population of *Drosophila*. *American Naturalist* **112**, 365-380.
- Heed, W.B. (1977) A new cactus-feeding but soil breeding species of *Drosophila* (Diptera: Drosophilidae). *Proceedings of the Entomological Society* **79**, 644-654.
- Heed, W.B. (1978) Ecology and Genetics of Sonoran Desert *Drosophila*. *Proceedings in the Life Sciences, Ecological Genetics: the Interface* (ed. P. F. Brussard), pp. 109-126. Springer, New York.
- Heed, W.B. (1982) The origin of *Drosophila* in the Sonoran Desert. *Ecological Genetics and Evolution: The Cactus-Yeast-Drosophila Model System* (eds J. S. F. Barker & W. T. Starmer), pp. 65-80. Academic Press, Sydney.
- Heed, W.B. & Mangan, R.L. (1986) Community ecology of the Sonoran Desert *Drosophila*. *The Genetics and Biology of Drosophila* (eds M. Ashburner, H. L. Carson & J. N. Thompson), pp. 311-345. Academic Press, London.

- Johnston, J.S. & Heed, W.B. (1975) Dispersal of *Drosophila*: the effect of baiting on the behavior and distribution of natural populations. *American Naturalist* **109**, 207–216.
- Johnston, J.S. & Heed, W.B. (1976) Dispersal of desert-adapted *Drosophila* the saguaro breeding *Drosophila nigrospiracula*. *American Naturalist* **110**, 629–651.
- Johnston, J.S. & Templeton, A.R. (1982) Dispersal clines in *Opuntia* breeding *Drosophila mercatorum* and *D. hydei* at Kamuela, Hawaii. *Ecological Genetics and Evolution: the Cactus–Yeast–Drosophila Model System* (eds J. S. F. Barker & W. T. Starmer), pp. 241–256. Academic Press, Sydney.
- Mangan, R.L. (1982) Adaptation to competition in cactus breeding *Drosophila*. *Ecological Genetics and Evolution: the Cactus–Yeast–Drosophila Model System* (eds J. S. F. Barker & W. T. Starmer), pp. 257–272. Academic Press, Sydney.
- McCauley, D.E. (1991) Genetic consequences of local population extinction and recolonization. *Trends in Ecology and Evolution* **6**, 5–8.
- McCauley, D.E. (1993) Genetic consequences of extinction and recolonization in fragmented habitats. *Biotic Interactions and Global Change* (eds P. M. Kareiva, J. G. Kingsolver & R. B. Huey), pp. 217–233. Sinauer Associates Inc., New York.
- Patterson, J.T. & Crow, J.F. (1940) Hybridization in the *Mulleri* group of *Drosophila*. *University of Texas Press* **4032**, 167–189.
- Patterson, J.T. & Wheeler, M.R. (1942) Description of new species of the subgenera *Hirtodrosophila* and *Drosophila*. *University of Texas Press* **4213**, 67–109.
- Pitnick, S. (1993) Operational sex ratios and sperm limitation in populations of *Drosophila packea*. *Behavioral Ecology and Sociobiology* **33**, 383–394.
- Rockwood-Sluss, E.S., Johnston, J.S. & Heed, W.B. (1973) Allozyme genotype–environment relationships. I. Variation in natural populations of *Drosophila packea*. *Genetics* **73**, 135–146.
- Roff, D.A. (1977) Dispersal in dipterans: its costs and consequences. *Journal of Animal Ecology* **46**, 443–456.
- Ruiz, A. & Heed, W.B. (1988) Host plant specificity in the cactophilic *Drosophila mulleri* species complex. *Journal of Animal Ecology* **57**, 237–249.
- Shorrocks, B. (1975) The distribution and abundance of woodland species of British *Drosophila* (Diptera: Drosophilidae). *Journal of Animal Ecology* **44**, 851–864.
- Sluss, E.S. (1975) *Enzyme variability in natural populations of two species of cactophilic Drosophila*. Ph D thesis, University of Arizona.
- Thompson, C.D. (1996) Essential ingredients of real metapopulations, exemplified by the butterfly *Plebejus argus*. *Aspects of the Genesis and Maintenance of Biological Diversity* (eds M. E. Hochberg, J. Clobert & R. Barbault), pp. 292–307. Oxford University Press, Oxford.
- Ward, B.L., Starmer, W.T., Russell, J.S. & Heed, W.B. (1975) The correlation of climate and host plant morphology with a geographic gradient of an inversion polymorphism in *Drosophila packea*. *Evolution* **28**, 565–575.
- Williams, G.M. (1987) *Techniques and Fieldwork in Ecology*. Bell & Hyman, London.
- Zouros, E. (1973) Genetic differentiation associated with the early stages of speciation in the *Mulleri* subgroup of *Drosophila*. *Evolution* **27**, 601–621.

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