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Dispersal in cactophilic *Drosophila*

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Three species of *Drosophila* each breed in necrotic tissue of specific columnar cacti endemic to the Sonoran Desert. *Drosophila pachea* breeds in senita (*Lophocereus schottii*), *D. nigrospiracula* breeds in saguaro (*Carnegiea gigantea*) or cardón (*Pachycereus pringlei*), and *D. mojavensis* uses organ pipe (*Stenocereus thurberi*) in Sonora, Mexico and southern Arizona. Patches of these three host cacti have very different spatial distributions, with those of senita being quite frequent and close together, while those of the other hosts are much father apart. Testing all three species simultaneously, we used capture-mark-release-recapture methods to ask if dispersal differed in these species and if differences were those predicted by the spatial availability of the host patches. *D. pachea* dispersed the shortest distance in all experiments. Furthermore, *D. pachea* was the only species showing sex-biased dispersal, with male flies exhibiting the greater propensity to disperse. The observations suggest that across similar spatial scales, *D. pachea* should show greater population genetic structure than the other two species, and that mitochondrial DNA, because of its maternal inheritance, might show greater evidence of structure than nuclear markers.

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In order for local genetic adaptations or differentiation to occur, there must be an absence or significant reduction in gene flow between local populations (Slatkin 1985, 1987). Gene flow, however, is not always easily measured, and its magnitude is often inferred from the degree of habitat patchiness (Shoemaker and Jaenike 1997) or from characters influencing mobility, such as winglessness (Peterson and Denno 1998a). In these cases, organisms using predictable patches are assumed to exhibit different dispersal rates compared to organisms whose resources are more patchy, i.e., less predictable or more widely dispersed. When dispersal truly correlates with factors such as habitat patchiness or winglessness, this assumption is valid. In contrast, when two species whose habitats are very different in patchiness exhibit equally strong levels of dispersal, patchiness may not be an appropriate indicator of expected genetic differentiation. Unless we know not only the degree of patchiness, but the relative dispersal as well, truly meaningful species comparisons of gene flow and genetic differentiation cannot be made.

Peterson and Denno (1998a, b) provide a statistical test of the relationship between dispersal or vagility and local genetic differentiation in their review of phytophagous insects. Their results showed that gene flow increases with mobility, but also that for more sedentary species, studies failing to incorporate a fine enough spatial scale will be unable to detect existing structure. These authors underscore the combined importance of using appropriate spatial scales and information about relative dispersal when comparing population structure across taxa.

Species of the genus *Drosophila* exhibit a wide range of genetic structure (reviewed in Nevo et al. 1984 and in Powell 1998), but these can only be subject to post hoc interpretation. One reason is the absence of the appropriate ecological framework in which to compare *Drosophila* species. Our knowledge of the relevant eco-

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logical parameters for *Drosophila* species has been too limited to allow a priori hypotheses about the relative degrees of population structure to be generated. While *Drosophila* hosts are known to include fruits, flowers, fungi, cacti, leaves, slime fluxes, and even land crabs (Carson 1971), those host characteristics with the potential to influence evolutionary processes (e.g. temporal and spatial distribution), have rarely been documented in a useful way.

The same is true of dispersal. Dispersal has been studied in a number of *Drosophila* species individually, but differences in techniques among studies preclude comparing them (reviewed in Powell 1998). The only general conclusion that can be drawn is that flies typically disperse long distances. Yet *Drosophila* species differ considerably in their degree of population structure. A priori tests of factors influencing population structure in *Drosophila* species cannot be constructed without knowledge of both the resource distributions and the dispersal rates for the species under investigation.

Drosophila species endemic to the Sonoran Desert of North America feed and breed in necrotic tissue of columnar cacti (Heed 1978). Each fly species is closely associated with a particular species of cactus and the spatial and temporal availabilities of necrotic patches recently have been reported to differ significantly among cactus species (Breitmeyer and Markow 1998). For populations of three species living in Sonora and Arizona, the host associations and patch densities are shown in Table 1. A fourth species, *D. mettleri*, breeds in moist soil under the necroses of all of these host cacti, but was not utilized in the study reported below. These differences in patch frequency allow us to test hypotheses, within an ecological framework, about the influence of resource distribution on population biology of the resident *Drosophila*. For example, in *D. nigrospiracula* and *D. mojavensis*, whose resources are infrequently encountered, we expect to see greater dispersal abilities or rates than in species like *D. pachea*, whose resources are frequent and close together. If the former could not disperse great distances, they would become extinct. For *D. pachea*, patches are abundant and close together across large areas, reducing the need to disperse to find suitable hosts.

Roff (1977) demonstrated in *D. melanogaster* that not only dispersal and body size show a positive relationship, but that a tradeoff exists between dispersal and egg production. Considerable body size differences exist among the cactophilic desert *Drosophila* species (Table 1). Heed and Mangan (1986) suggested that the large body size of *D. nigrospiracula* was important in the ability of these flies to disperse. Unfortunately, dispersal was only examined in this one cactophilic desert species (Johnston and Heed 1975, 1976), and the relative dispersal of the others is unknown. Dispersal based upon size alone would produce interspecific differences in which *D. nigrospiracula* is the strongest disperser and *D. mojavensis*, the smallest bodied species, disperses the shortest distances. Thus resource distribution and body size hypotheses of dispersal in these species yield contrasting predictions.

With respect to potential energetic tradeoffs, the desert species provide an interesting contrast to *D. melanogaster*. The desert species exhibit considerable sex differences in allocation to reproduction. This difference has reached an extreme in *D. pachea*, where the investment in testes, associated with the production of giant sperm, causes males to reach sexual maturity nearly two weeks later than their sisters (Pitnick 1996, Pitnick and Markow 1994). Whether investment in testes is similar to investment in ovaries with respect to a tradeoff for dispersal has never been addressed. If a sex difference in dispersal is found, however, in any of these species, it should manifest itself in female-biased dispersal in *D. pachea*.

There have been no comparative population genetic studies of these cactophilic species. The one species, *D. pachea*, for which allozyme (Rockwood-Sluss et al. 1973) and chromosomal inversion frequencies (Ward et al. 1974) have been studied yielded somewhat different pictures about local differentiation. Information about spatial resource distribution and dispersal would allow us to generate a priori hypotheses about the comparative population genetics of these species.

Below we describe experiments in which we ask 1. Do *D. nigrospiracula*, *D. mojavensis*, and *D. pachea* differ in their dispersal distances and, if so, do the differences conform to the predictions of the resource distribution or body size models?, and 2. Are there sex

Table 1. Three species of desert *Drosophila*, their host plants in Sonora, Mexico, and Arizona, USA and the relative densities of host patches. F: female, M: male.

Species	Primary host in Sonora and Arizona	Patches/ha*	Fly thorax length (mm)**
D. nigrospiracula	Cardón (*Pachycereus pringlei*) Saguaro (*Carnegiea gigantea*)	0.4 0.1	1.42 F 1.27 M
D. pachea	Senita (*Lophocereus schottii*)	1.8	1.12 F 1.02 M
D. mojavensis	Organpipe (*Stenocereus thurberi*)	0.1	0.96 F 0.89 M

* Breitmeyer and Markow 1998.
** Pitnick et al. 1995.

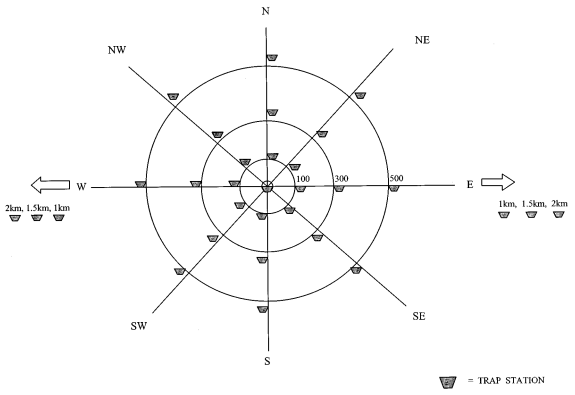

Fig. 1. Description of the positions and distances of the trap stations used in release-recapture experiments. The center is referred to as the origin.

differences in dispersal and, if there are, do they conform to predictions based upon investment in reproduction? Our goal was not to obtain precise estimates of how far individuals of each species disperse, as this is known to be affected by a suite of biotic and abiotic factors (Powell 1998). Rather, we were interested in two things: whether the predicted sex and species differences exist and whether observed differences allow predictions to be made about the comparative population biology of these species. We were able to address these goals using capture-mark-release-recapture methods to simultaneously measure dispersal in males and females of all three species.

Methods

Three capture-mark-release-recapture experiments were conducted, all in the same location. Experiment one was conducted in February 1996, and experiments two and three were done in February 1997, several days apart. In experiment one, in 1996, it was only possible to examine two species, *D. nigrospiracula* and *D. pachea*. The following year, in 1997, we were able to collect sufficient numbes of *D. mojaensis*, in addition to the other two species, to conduct two experiments, both of which used all three species.

Release-recapture area

An area (5 km^2) near San Carlos, Sonora, Mexico, was selected for the study area for all three experiments reported below. The area was large enough to permit the placement of eight trap lines (Fig. 1). All eight lines had trap stations at 100, 300, and 500 m from the origin, where there was also a trap station. Two of the trap lines, W and E, had additional trap stations at 1000, 1500, and 200 m from the origin. The distances at which trap stations were placed were determined on the basis of preliminary release-recapture studies with these species.

Traps

Plastic ice cream buckets, the lids of which were cut to provide 7-cm-diameter holes, were used as traps. Each bucket was provisioned with approximately 1 kg of necrotic senita, cardón or organpipe cactus. At each station, single buckets of each cactus type used by the species being released were placed within 1 m of each other and positioned such that each bucket was partially shaded. Thus in 1996, when the release included only *D. nigrospiracula* and *D. pachea*, each trap station had a bucket with cardón and a bucket with senita. In both 1997 experiments, in which *D. mojavensis* was also released, a third bucket, containing necrotic organpipe, was included at each trap station.

Necrotic tissue of each species of cactus was created by taking fresh cactus and cutting it into pieces approximately 5–10 cm^3. The pieces were placed, separately by species, in special fermenting tubs. Naturally occurring necroses of each species were located in the field and served as sources of the host-specific microbial communities used to inoculate the tissue in the tubs. The necroses used for inoculation had *Drosophila* associated with them, so they were clearly attractive to flies. Before using the necrotic material for inoculation, however, all life stages of any arthropods were carefully removed. Tubs thus were set up with fresh cactus tissue, necrotic material, and water one week before each experiment, and stirred daily to ensure even exposure of all pieces to the necrotic broth.

Collection and preparation of flies

Flies of each species were collected using nets and aspirators from active necroses on their host plants. The collection sites were located approximately 25 km from the release area. Before preparing them for release, fly species identity was verified and the numbers of each sex determined. These identifications were done without anesthesia by transferring small numbers of flies to narrow glass tubes that were examined under a microscope. These cactophilic *Drosophila* species are very host specific, but occasionally adults will be found feeding on each other's hosts. To rule this out in our collections we took two precautions. A subsample of each collection was anesthetized and keyed out to check the accuracy of our unanesthetized determinations. The only flies that could not be verified in this way were females of *D. arizonae*, the sibling species of *D. mojavensis*. Culturing sets of isofemale lines from these subsets revealed not a single *D. arizonae* female and no

males were observed in the subsample. Collections of *D. nigrospiracula* often contain *D. mettleri*, the males of which are easily distinguished on the basis of their unique genitalia. Male flies identified as *D. mettleri* were removed from the pre-release collections. Females can only be distinguished by the bristles on their heads, and therefore we had to rely on the anesthetized subsamples to assess the potential numbers of *D. mettleri* females in the collections. No collection contained more than 3% *D. mettleri* females and the values for the *D. nigrospiracula* release groups were corrected to reflect this proportion. No *D. mettleri* were found in the collections of the other two species.

Flies were collected in the morning and brought to the laboratory to be examined and marked. After the numbers of males and females of each species had been counted and individuals of the wrong species removed, flies were dusted with micronized fluorescent dusts of different colors. These dusts (Radiant Corp., Richmond, CA) are those typically used in *Drosophila* dispersal studies (Crumpacker and Williams 1973) because they do not affect the health or movement of the flies. Different colors were used for different species. After dusting, flies were allowed to clean themselves, in low density bottles, for 24 h before their release. The following afternoon, they were released from these bottles at the origin.

Collection and analysis of recaptured flies

For all three experiments, collections were made of all marked and unmarked flies at each trap station at 24 h and again 48 h after each release. If a necrotic cactus was present in the area at the time of the experiment, any flies found there were collected as well. Flies were taken to the laboratory in Guaymas where they were anesthetized, identified, and counted and scored for colored dust. No marked flies were recovered from necrotic cacti.

To test for differences between recapture distributions, we used a Komolgorov-Smirnov two-sample test. This test generates a χ^2 value using $df = 2$ and is conservative in cases when samples sizes are below 40 and $n_1 \neq n_2$ (Siegel 1956).

Results

Species differences in dispersal

Total numbers of flies of each sex released and recaptured in each of three experiments, along with temperatures and wind speeds, are presented in Table 2. A total of 3632 flies of three species were released with a total recapture rate of 10.5%. Recapture rates were similar for all three species.

We first asked, using the Komolgorov-Smirnov two sample test, if data from the first and second days of recapture were homogeneous. While the flies in the second collection were slightly farther from the origin than those recaptured the first day, in no case were these differences significant. The distributions and means shown in Fig. 2 and Table 3, respectively, by experiment, are therefore based on recaptured flies from both days. Results are presented for each experiment separately because recapture distances differed among releases and our interest was in whether species showed consistent differences in relative recapture distances from experiment to experiment.

In the first experiment, *D. nigrospiracula* moved significantly farther than *D. pachea*, both on the basis of their distributions (Fig. 2a; K-S $\chi^2 = 22.6$, $p < 0.001$) and their mean distances (Table 3) from the origins. This same difference was also observed in distributions in the second (K-S $\chi^2 = 7.15$, $p < 0.05$) and third (K-S $\chi^2 = 8.85$, $p < 0.02$) experiments (Fig. 2b, c), which also included *D. mojavensis*. Mean distances for *D. nigrospiracula* and *D. mojavensis* were placed in the same subset by a Duncan multiple range test ($\alpha = 0.5$), separate from *D. pachea* in both 1997 experiments. Observations on *D. mojavensis*, however, differed somewhat between the two experiments in which it was included. In the first 1997 release, a large proportion of recaptured flies of *D. mojavensis* was found at the origin. As can be seen in Fig. 2b, however, a sizeable number was also recaptured at an even greater distance from the origin than *D. nigrospiracula*. This distribution no doubt accounts for the fact that in experiment two, *D. mojavensis* did not differ significantly in the Komolgorov-Smirnov test from *D. pachea* ($\chi^2 = 1.78$), but was different from *D. nigrospiracula* ($\chi^2 = 7.40$, $p < 0.05$). In the second 1997 experiment, *D. mojavensis* and *D. pachea* were significantly different ($\chi^2 = 6.46$, $p < 0.05$), but *D. mojavensis* and *D. nigrospiracula* did not differ ($\chi^2 = 1.72$). *Drosophila mojavensis* clearly has the potential to disperse farther than either of the other two species.

While flies of all species dispersed farther in the third experiment, differences between species were consistent from experiment to experiment. *Drosophila nigrospiracula* and *D. mojavensis* move consistently father than *D. pachea*, but their movements are similar to each other. Because *D. nigrospiracula* and *D. mojavensis* are the largest and smallest flies, respectively, it is unlikely that body size is the most important factor determining species differences in dispersal distance. On the other hand, the necrotic patches utilized by these two species are farther apart in nature than are those of *D. pachea*. The results are more consistent, therefore, with a relationship between dispersal and resource distribution than with body size.

Table 2. Numbers of flies released and recaptured and the wind and temperature conditions for each experiment. Temperatures and wind speeds for the two recaptures in each experiment showed negligible variation and are therefore presented together.

Species	Expt	Released			Wind (m/s)	Temp. (°)	Recaptured				Wind (m/s)	Temp. (°)
		♀♀	♂♂	Total			♀♀	♂♂	Total	%		
D. nigrospiracula	1	406	440	846	S 3	24	56	47	103	12.2	S 1-5	23.5–25
	2	231	304	535	SW 3	23.5	38	42	80	15.0	SW 1-3	23–24.5
	3	130	172	302	SW 1	25.5	11	12	23	7.6	SW 1-3	24.5–27
D. pachea	1	367	353	720	S 3	24	24	13	37	5.1	S 1-5	23.5–25
	2	88	152	240	SW 3	23.5	14	17	31	12.9	SW 1-3	23–24.5
	3	91	154	245	SW 1	25.5	14	17	31	12.6	SW 1-3	24.5–27
D. mojavensis	2	239	233	472	SW 3	23.5	27	36	64	13.6	SW 1-3	23–24.5
	3	132	140	272	SW 1	25.5	6	11	17	6.2	SW 1-3	24.5–27

Sex differences in dispersal

In order to test for sex differences in dispersal, sex differences in recapture rates were first ruled out (Table 4). When the numbers of flies recaptured were partitioned by sex, the sample sizes became substantially reduced. We therefore examined sex differences in dispersal by asking, simply, if the numbers of males and females recaptured at the origin vs the other recapture stations were different. In two cases, both involving *D. pachea*, there were significantly more males than females captured at stations away from the origin (Table 2). For *D. nigrospiracula* and *D. mojavensis*, no sex differences were found.

Active vs passive dispersal

Table 5 shows the distribution of marked, recaptured flies and unmarked flies attracted to the baits at each of the collection stations, according to the direction from the origin. These data address two issues. First, they demonstrate that stations in given areas are not simply more suitable locations for *Drosophila* or more attractive to flies than those stations in other directions. All areas attracted large numbers of wild *Drosophila* of the three species of interest.

Second, the distributions of recaptured flies, in several cases, do not appear to be random in terms of direction from the release point. As this lack of randomness is obviously not a function of greater attractiveness or suitability of these areas, other factors must be responsible. The most obvious potential explanation is passive dispersal, as a function of wind direction. Direction and speed of wind was recorded at the times of release and recapture (Table 2). In 1996, the majority of recaptured flies were at stations N, NE, and E of the origin, while in 1997, the majority of flies were found S, SW, and W of the origin. In all three experiments, wind was recorded out of the south to southwest. In 1996, passive dispersal would have sent the recaptured flies to the north and northeast. While a considerable number of flies were recaptured in the N and NE stations, the largest number was found in the east. In the 1997 experiments, flies appear to have actually moved upwind from the release point. We conclude that passive, windborn dispersal is unlikely to be the primary explanation for the nonrandom distributions observed, especially in 1997.

Discussion

Species differences

Our results represent the first comparative dispersal data set for *Drosophila* based upon a priori hypotheses rooted in the resource ecologies of the species of inter-

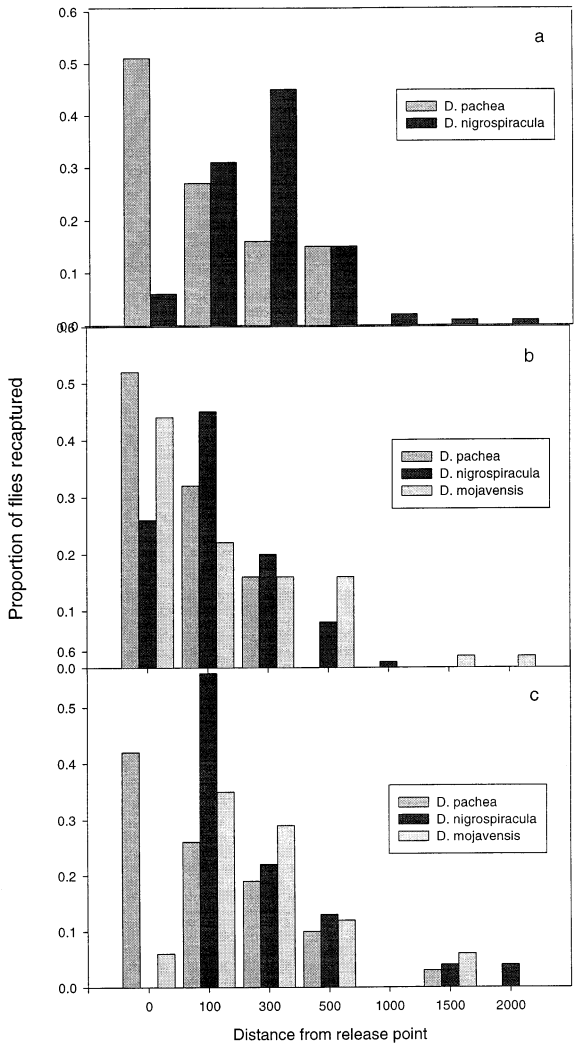

Fig. 2. Distances from the release point of recaptured flies. (a) 1996 average distances (m) for *D. pachea* 102.7 ± 23.7, *D. nigrospiracula* 289.3 ± 27.2; (b) 1997 – experiment 1 average distances (m) *D. pachea* $80.6 + 19.4$, *D. nigrospiracula* 152.5 ± 19.3, *D. mojavensis* 201.6 ± 42.2; (c) 1997 – experiment 2 average distances (m) *D. pachea* 180.6 ± 53.0, *D. nigrospiracula* 339.1 ± 98.9, *D. mojavensis* 329.4 ± 83.9.

est. Species differences observed are consistent with the spatial distributions and predictabilities of the specific host patches utilized by these species. *Drosophila pachea* exhibited significantly lower dispersal relative to *D. nigrospiracula* in all three release experiments. Results for *D. mojavensis*, available for only two releases, while somewhat different between experiments, indicate that flies of this species exhibit dispersal distances similar to *D. nigrospiracula*. Senita cacti and their necroses, the breeding sites of *D. pachea*, are much more dense and more frequently encountered than the hosts of the other two species.

A number of factors have been shown to influence results of dispersal studies in *Drosophila*. Our design, in which baits consisted of necrotic material of the species' natural hosts and simultaneous multispecies releases, avoided the confounding problems of differential attractiveness of artificial *Drosophila* baits (Johnston and Heed 1975), and of making species comparisons on data collected between, rather than within, experiments. Another potential complication identified in previous studies is that of the number of flies released and the effect of potential crowding on disturbance and subsequent dispersal (Wallace 1966, Powell et al. 1976, Begon 1976). In our study, flies were released from multiple holding bottles of low density rather than from containers housing large numbers of flies, which is probably why our data were not confounded by any correlation between number of flies released and either recapture rate or distance dispersed.

Recapture rates reported here ($\approx 10\%$) are similar to those reported in previous studies on *Drosophila* dispersal (Powell et al. 1976, Worthen 1989). Those differences in methods and design, however, which preclude comparison of dispersal distances reported among these studies, also mitigate comparison between the species reported upon here and those in the previous reports. As data on natural hosts and their distributions are generated for other *Drosophila* species, the design employed here should be useful in comparative dispersal studies of *Drosophila* species utilizing those hosts. The use of an index species common to all experiments allows more meaningful comparisons across studies.

Two species of *Drosophila* in this study, *D. nigrospiracula* and *D. mojavensis*, utilize different host cacti in Baja California. Observations of Mangan (1982) suggest that patches of agria (*Stenocereus gummosis*), the Baja California host of *D. mojavensis*, are likely to occur at greater densities than those of organpipe. Baja populations of *D. mojavensis*, therefore, should be examined to see if their relative dispersal is reduced, as predicted by the results of the present study. Saguaro does not occur in Baja California (Turner et al. 1995), where *D. nigrospiracula* instead utilize necrotic cardón exclusively. The cardón in Baja

Table 3. Mean distances from origin at which flies were recaptured.

Experiment	Species	$X \pm$ SE (n) meters from origin
1. February 1996	*D. nigrospiracula*	289 ± 27 (103)
	D. pachea	102 ± 24 (37)
2. February 1997	*D. nigrospiracula*	152 ± 19 (80)[b]
	D. pachea	80 ± 19 (31)[a]
	D. mojavensis	201 ± 42 (64)[b]
3. February 1997	*D. nigrospiracula*	339 ± 99 (23)[b]
	D. pachea	180 ± 53 (31)[a]
	D. mojavensis	329 ± 84 (17)[b]

a,b designate different subsets from a Duncan multiple range test ($\alpha = 0.05$).

Table 4. Chi square tests for sex differences in total recapture rates and for sex differences in those flies dispersing versus those remaining at the origin.

Species	Release	χ^2: Sex release vs recapture	χ^2: Sex origin vs away
D. nigrospiracula	2/96	1.72	1.06
	2/97-1	0.52	0.25
	2/97-2	0.22	1.03
D. pachea	2/96	2.73	0.16
	2/97-1	0.71	4.35*
	2/97-2	0.75	5.19**
D. mojavensis	2/97-1	1.81	0.0
	2/97-2	1.64	2.34

* $p < 0.05$.
** $p < 0.02$.

California, however, are very different in growth form than those on the mainland, having smaller circumferences and fewer arms. Whether there is a difference in Baja in the incidence of cardón necroses is unknown. If cardón patch frequency does differ in Baja, it would provide an additional opportunity to test the apparent relationship between host distribution and dispersal ability.

Sex differences

Our prediction that if sex differences in dispersal were found, they would be most pronounced in *D. pachea* where males would have less energy for dispersal, was fulfilled, but in the opposite direction than we expected. Males, despite an investment in testes associated with a significant delay in reproductive maturity (Pitnick, 1996, Pitnick and Markow 1994), moved significantly farther than females in two of three experiments. No sex differences were found in the other two species, in which male maturity, relative to females, is delayed to a lesser extent. Other *Drosophila* species in which there has been evidence of sex biased dispersal are *D. pseudoobscura* (Powell et al. 1976) and *D. subobscura* (Begon 1976), in which males appeared to disperse farther. McKenzie (1974), however, reported no differences for *D. melanogaster* and *D. simulans*. In *D. engyochracea*, a Hawaiian species, Fontedevilla and Carson (1978) reported greater female dispersal.

While a clear tradeoff between egg production and dispersal has been demonstrated in *D. melanogaster* (Roff 1977) and other insects (Johnson 1963), our findings suggest that without additional information, it may not be appropriate to assume the same tradeoff exists for males. In species such as *D. pachea*, where sperm production costs are high, gametogenesis may compete for different internal resources in males than in females (Markow et al. 1999). As with egg production, the influence of flight on testes development can be directly assessed in the laboratory. The ages at which *Drosophila* males and females of various species disperse, relative to attainment of reproductive maturity, is more difficult to address but represents an important area of inquiry that may reflect different evolutionary and ecological constraints.

Implications for population biology

Regardless of the mechanisms or factors underlying species and sex differences in dispersal, our findings provide an important framework for future population genetic and ecological physiology studies. The clear

Table 5. Distributions at capture locations of marked and unmarked flies in three release-recapture studies. N = *D. nigrospiracula*, P = *D. pachea*, M = *D. mojavensis*. UNM = unmarked flies of all species.

	1996			1997-1				1997-2			
Location	N	P	UNM	N	P	M	UNM	N	P	M	UNM
S	3	1	6	14	1	5	73	4	2	2	70
SW	5	0	3	7	2	5	85	3	3	1	58
W	6	0	9	23	3	6	74	4	7	2	56
NW	10	4	7	9	2	5	75	2	1	4	83
N	16	3	3	5	1	3	59	5	0	1	55
NE	20	5	11	0	4	4	79	1	1	1	78
E	30	2	6	0	1	1	65	3	4	4	65
SE	11	3	5	1	1	6	77	1	0	2	91
O	2	19	3	21	16	28	61	0	13	0	55
Total	103	37	53	80	31	63	648	23	31	17	611

relationship between population genetic differentiation and dispersal in phytophagous insects (Peterson and Denno 1998a, b) suggests that, when examined at the appropriate spatial scales, the degree of genetic differentiation among these three cactophilic species will also differ in predictable ways. *Drosophila nigrospiracula* and *D. mojavensis* are expected, from the northern limit of their range in southern Arizona to the southern limit in northern Sinaloa, to show less population subdivision than *D. pachea*. Additionally, the more restricted dispersal of female *D. pachea*, relative to males, suggests the potential for mitochondrial variation to show greater population subdivision than nuclear variation in this species.

Unfortunately, the comparative population genetics of these species have never been examined. No data are published for *D. nigrospiracula*. Earlier allozyme studies of *D. mojavensis* (Zouros 1973) and allozyme and chromosome studies of *D. pachea* (Rockwood-Sluss et al. 1973, Ward et al. 1974, Duncan 1979) suggest that variability may be lower in these species compared to other *Drosophila* species, but at least for *D. pachea*, some evidence of local differentiation for nuclear loci exists. A large-scale comparative study can now be undertaken to characterize the genetic structure of these species in a meaningful ecological and biological framework.

Finally, species differences in dispersal raise important questions about the physiology of these species. In addition to the implications of sex differences in resource allocation discussed earlier, nothing is known about flight ability in these species. Based upon the differences in dispersal and resource distribution, flies of *D. nigrospiracula* and *D. mojavensis* are expected to be able to fly greater distances than those of *D. pachea*. Greater desiccation resistance in *D. nigrospiracula* and *D. mojavensis* is also predicted, as flies of these species are exposed to ambient conditions for longer dispersal periods because their patches are farther apart. Our laboratory is currently testing the genetic and physiological predictions generated by the observations reported above.

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