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Ecology and population genetics of Sonoran Desert *Drosophila*

E. PFEILER* and T. A. MARKOW†
*Department of Biology, Arizona State University, Tempe, AZ 85287 USA, †Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ 85721, USA

Abstract

Three species of cactophilic *Drosophila* endemic to the Sonoran Desert of North America, *D. nigrospiracula*, *D. pachea* and *D. mettleri*, experience marked differences in spatial resource availability, and the first two of these display significant differences in dispersal behaviour. We employed starch gel and cellulose acetate electrophoresis for eight allozyme loci to test for a relationship between these variables and genetic differentiation among geographical populations of each species. No evidence was found for population structure in any of the three species, populations of which were separated by geographical distances of up to 475 km. Allele frequencies for two loci, *Mdh-1* and *Est-2*, in *D. nigrospiracula* and *D. pachea* were very similar to those obtained ≈ 30 years ago by other workers, indicating that the polymorphisms are remarkably stable under the stressful and variable conditions of the desert environment. High longevity, dispersal and multiple female remating are likely to contribute to the apparent high level of gene flow in all three species.

Keywords: allozyme, *Drosophila mettleri*, *Drosophila nigrospiracula*, *Drosophila pachea*, genetic variability, population structure

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Introduction

Despite the large number of studies of genetic variation in various *Drosophila* species (reviewed in Nevo *et al*. 1984 and Powell 1997), few have been undertaken to test proposed relationships between ecological variables and population genetics (Lacy 1983; Jaenike 1989; Thomas & Barker 1990; Santos 1997; Shoemaker & Jaenike 1997). The lack of a priori hypothesis testing no doubt reflects the absence of appropriate ecological and population biological data for most *Drosophila* species generating predictions about their genetics. One group of four *Drosophila* species, each breeding in specific necrotic columnar cactus endemic to the Sonoran Desert of North America (Heed 1978; also see Table 1), has recently been found to differ considerably in typical population size, spatial resource distribution (Breitmeyer & Markow 1998) and dispersal behaviour (Markow & Castrezana 2000).

Population genetic data for these four species of *Drosophila* (*D. nigrospiracula*, *D. pachea*, *D. mettleri* and *D. mojavensis*) are sparse. Only for *D. mojavensis* has a sufficiently large number of loci been screened to permit estimates of genetic variability (Zouros 1973) or population subdivision (Zouros 1973; G. D. Hocutt & T. A. Markow, manuscript submitted). In an allozyme study, Zouros (1973) found *D. mojavensis* to be less variable than other related nondesert species. One small allozyme study on *D. pachea* found that observed heterozygosity was within the range reported for other *Drosophila* species, but closer to the lower end of that range (Rockwood-Sluss *et al*. 1973). Based upon these observations, and the specificity of the cactophilic desert niche, Johnston & Heed (1976) suggested that low variability is typical of the four species as a group. The scant data addressing this suggestion, however, suggest that this conclusion may be premature.

Two of the cactophilic species, *D. nigrospiracula* and *D. pachea*, contrast markedly in ecology and population biology (Breitmeyer & Markow 1998). With respect to resource availability, necrotic patches or 'rots' of the two hosts of *D. nigrospiracula* (saguaro and cardón) occur far less frequently and at greater distances than necrotic patches of senita, the host of *D. pachea* (Table 1). The two species also differ dramatically in their average population

Correspondence: T.A. Markow. Fax: 1-520-626-3522; E-mail: tmarkow@arl.arizona.edu

Table 1 Summary of host plant associations in the state of Sonora, resource availability, population sizes, and dispersal capabilities of four species of cactophilic *Drosophila*

Drosophila species	Host cactus	Resource availability* (rots/ha)	Population size† (flies/rot) (*N*)	Dispersal distance‡ (m/day)
D. nigrospiracula	cardón (*Pachycereus pringlei*)	0.4 ± 0.1	5123 ± 1713 (18)	260 (100–2000)
	saguaro (*Carnegiea gigantea*)	0.1 ± 0.0		
D. pachea	senita (*Lophocereus schottii*)	1.9 ± 0.4	399 ± 238 (15)	121 (100–500)
D. mettleri	(soil soaked with necrotic juices of any of these hosts)§	§	1198 ± 235 (13)	No data
D. mojavensis	organ pipe (*Stenocereus thurberi*)	0.1 ± 0.0	5352 ± 1923 (3)	265 (100–2000)

*Mean rot densities (± SE) for cardón, senita and organ pipe cacti were from 12 surveys taken at different times of the year (August, November, February and May) over a 3-year period on a 15 ha site at Guaymas, Sonora; data for saguaro are from a study site near the Lost Dutchman Mine, Superstition Mountains, Arizona (from Breitmeyer & Markow 1998). †Mean population size (± SE) at a single necrosis obtained during November, February and May (no flies were found in August). *N* = Number of population estimates conducted for each species. Census data for individual species from different localities were pooled (from Breitmeyer & Markow 1998). ‡Mean dispersal distance (range in parentheses) from three different experiments for *D. nigrospiracula* and *D. pachea*, and two experiments for *D. mojavensis* (from Markow & Castrezana 2000). §*D. mettleri* breeds in soil soaked with rotting juices from organ pipe, although cardón and saguaro are the most common hosts.

sizes, with the mean number of flies found at a single rot being > 10-fold higher in *D. nigrospiracula* than in *D. pachea* (Table 1). Finally, adult *D. nigrospiracula* disperse considerably farther than those of *D. pachea* (Table 1). These observations, taken together, predict that if these two species differ in their population genetics, populations of *D. nigrospiracula* should exhibit greater genetic variability and less structure than *D. pachea*. Unfortunately, previous studies on the population genetics of these two species examined only a few loci, two in *D. nigrospiracula* (Sluss 1975) and four in *D. pachea* (Rockwood-Sluss *et al*. 1973). Although no evidence was found for population structure in either species, the robustness of the conclusion is weakened by the limited number of loci examined. Furthermore, in *D. pachea*, considerable differentiation has been reported among populations for the 7A and 7+ chromosomal gene arrangements (Ward *et al*. 1975; Duncan 1979) suggesting that additional genetic studies, utilizing more loci, may indeed reveal population structure for this species.

Information on population genetics of the third cactophilic species treated here, *D. mettleri*, is completely lacking. *D. mettleri* is less specific in its host requirements in that it breeds in soil soaked with the necrotic juices of several host cacti (Table 1). Although no information is available on the dispersal capability of *D. mettleri*, population size per rot averages ≈ 1200 (Table 1).

In this study we screened eight enzyme loci in *D. nigrospiracula*, *D. pachea* and *D. mettleri* to ask: (i) whether these three species show reduced genetic variability compared with nondesert *Drosophila* species; and (ii) to what degree resource availability and dispersal behaviour predict genetic structure among geographically distant populations. No evidence for population structure, over a distance of almost 500 km, was found for any of the three species. Average heterozygosity varied slightly in the three species, but values were close to the average values reported for nondesert *Drosophila*.

Materials and methods

Collection of flies

Adult flies were collected from three different geographical localities within the Sonoran Desert [Guaymas, Sonora, Mexico; Organ Pipe Cactus National Monument (OPNM), Arizona; and Tucson, Arizona] from March to May 1998 and February to June 2000. The distance from both Tucson and OPNM to Guaymas is ≈ 475 km; the Tucson and OPNM sites are separated by ≈ 180 km. *Drosophila nigrospiracula* and *D. mettleri* were collected from all three localities in association with necrotic tissue of their host cacti, saguaro at Tucson and OPNM and cardón at Guaymas (saguaro is also present at Guaymas, but rots are not abundant). *D. pachea* was collected from two sites, OPNM (the northernmost distributional limit of its host cactus, senita) and Guaymas.

Allozyme electrophoresis

Male and female flies were separated and then homogenized individually in 25 μL of grinding buffer (Cleland *et al*. 1996). Homogenates were centrifuged for 5 min at 10 000 ***g*** and the supernatants analysed by electrophoresis either on 12.5% starch gels (Starch Art Corp., Smithville, TX, USA) or Titan III cellulose acetate plates (Helena Laboratories, Beaumont, TX, USA). Gel electrophoresis was carried out at 4 °C in a buffer system of 40 mM citrate adjusted to pH 6.0 with *N*-(3-aminopropyl)morpholine (diluted 1:20 in the gel). After electrophoresis, gel slices were stained for

enzyme activity using standard recipes (Murphy *et al*. 1990). Cellulose acetate electrophoresis was performed for 20 min (22 °C) at 200 V using Tris-glycine buffer (pH 8.0); enzyme staining followed the recipes given in Hebert & Beaton (1989) with minor modification.

The enzymes (with abbreviations and EC numbers) analysed in the three species were phosphoglucomutase (PGM; EC 5.4.2.2) alcohol dehydrogenase (ADH; EC 1.1.1.1), malate dehydrogenase (MDH; EC 1.1.1.37), glycerol-3-phosphate dehydrogenase (NAD^+) (GPDH; EC 1.1.1.8), cytosol nonspecific dipeptidase (PEP-A; EC 3.4.13.18; glycylleucine substrate), tripeptide aminopeptidase (PEP-B; EC 3.4.11.4; leucylglycylglycine substrate), arginine kinase (ARGK; EC 2.7.3.3) and carboxylesterase (EST; EC 3.1.1.1; α-napthylacetate substrate). The loci coding for these enzymes are abbreviated and given in italics.

Because the *Pgm* locus was previously found to be sex-linked in *D. pachea* (Pfeiler & Markow 2000), only females were scored for this locus in this species. Also, ADH is not expressed in mature adult males of *D. pachea* (Pfeiler & Markow 2001), therefore the data set for this enzyme in *D. pachea* also included only females. In all other instances, allele frequency data are for the two sexes combined. With a few exceptions, the number of flies of each species from each locality analysed ranged from 30 to 70.

Statistical analyses

Estimates of genetic variation and Wright's *F*-statistics were performed with BIOSYS-1 (Swofford & Selander 1989). The calculation of significance of pairwise comparisons of F_{ST} for each species was performed using ARLEQUIN version 1.1 (Schneider *et al*. 1997) with 1000 permutations of the data matrix.

Results

Allele frequencies for all polymorphic loci and localities were in Hardy–Weinberg equilibrium (HWE), except *Pep-B* in *Drosophila nigrospiracula* from Guaymas and *D. mettleri* from Tucson. In the latter, the presence of a single heterozygote containing two rare alleles caused the deviation from equilibrium. ARGK was the only enzyme that was monomorphic in all three species. In addition, ADH was monomorphic in *D. pachea*. Genetic variability, as reflected in heterozygosity, mean number of alleles per locus, and per cent polymorphic loci (95% criterion), was similar in the three species (Table 2), although *D. mettleri* appeared slightly less variable. Furthermore, *D. pachea* from OPNM, although representing a population from the northernmost margin of this species' range, was no less variable than the more central population in Guaymas.

No population subdivision was detected among populations of any of the three species. Despite a geographical distance of 475 km, as well as being limited to a single host (saguaro) in Tucson, *D. nigrospiracula* and *D. mettleri* exhibited overall F_{ST} values of 0.013 and 0.012, respectively (Table 3). Populations of *D. pachea* from Guaymas and OPNM were essentially identical ($F_{ST} = 0.002$). Pairwise comparisons of F_{ST} for each species indicated that none of the values were significant at the 5% level. Pairwise genetic distance values (Nei 1978; unbiased) in the three species ranged from 0.000 to 0.003.

Discussion

We found no evidence to support earlier suggestions (Johnston & Heed 1976) that genetic variability is low in desert-adapted *Drosophila*. Levels of observed heterozygosity for *D. nigrospiracula* (0.14–0.16), *D. pachea* (0.17) and *D. mettleri* (0.09–0.13) were in the middle of the range found for nondesert species of *Drosophila* (Ayala *et al*. 1974; Nevo 1978). Previously estimated heterozygosity for *D. pachea*, also based on eight loci that were not specified, was 0.12 (Rockwood-Sluss *et al*. 1973), slightly lower than our estimate. The only desert *Drosophila* in which there

Table 2 Summary of genetic variability in Sonoran Desert populations of *Drosophila nigrospiracula*, *D. pachea* and *D. mettleri*

Species	Locality (*N*)*	H_O (± SE)†	H_E (± SE)‡	Mean no. alleles per locus (± SE)	% polymorphic loci (95%)
D. nigrospiracula	Guaymas (8)	0.142 (± 0.083)	0.160 (± 0.086)	2.63 (± 0.84)	37.5
	OPNM§ (8)	0.141 (± 0.069)	0.146 (± 0.071)	2.75 (± 0.65)	37.5
	Tucson (8)	0.158 (± 0.076)	0.170 (± 0.086)	2.88 (± 0.77)	37.5
D. pachea	Guaymas (8)	0.174 (± 0.075)	0.179 (± 0.075)	2.50 (± 0.42)	50.0
	OPNM (8)	0.169 (± 0.078)	0.169 (± 0.079)	2.25 (± 0.45)	50.0
D. mettleri	Guaymas (8)	0.125 (± 0.069)	0.112 (± 0.058)	2.63 (± 0.63)	50.0
	OPNM (8)	0.094 (± 0.057)	0.086 (± 0.050)	1.88 (± 0.35)	12.5
	Tucson (8)	0.104 (± 0.050)	0.111 (± 0.056)	2.63 (± 0.46)	27.5

*N = total number of enzyme loci; †H_O = observed heterozygosity (direct count); ‡H_E = Hardy–Weinberg expected heterozygosity, unbiased estimate (Nei 1978); §OPNM = Organ Pipe Cactus National Monument.

Table 3 Summary of Wright's *F*-statistics* in polymorphic loci of Sonoran Desert populations of *Drosophila nigrospiracula*, *D. pachea* and *D. mettleri*

Species	Locus	F_{IS}	F_{IT}	F_{ST}
D. nigrospiracula	*Pgm*	−0.013	−0.007	0.007
	Adh	−0.020	−0.017	0.003
	Mdh-1	−0.070	−0.061	0.008
	Gpdh	−0.017	−0.009	0.008
	Pep-A	−0.019	−0.017	0.002
	Pep-B	0.276	0.288	0.016
	Est-2	0.053	0.067	0.015
Mean		0.060	0.072	0.013
D. pachea	*Pgm*	0.071	0.071	0.000
	Mdh-1	−0.036	−0.035	0.001
	Gpdh	−0.010	−0.005	0.005
	Pep-A	−0.068	−0.057	0.011
	Pep-B	−0.028	−0.028	0.001
	Est-2	0.043	0.044	0.001
Mean		0.002	0.004	0.002
D. mettleri	*Pgm*	−0.039	−0.029	0.010
	Adh	−0.085	−0.070	0.014
	Mdh-1	−0.011	−0.004	0.007
	Gpdh	−0.007	−0.002	0.005
	Pep-A	−0.056	−0.023	0.031
	Pep-B	0.015	0.017	0.002
	Est-2	0.043	−0.040	0.003
Mean		−0.060	−0.048	0.012

*Wright (1978).

is evidence of relatively lower genetic variability is *D. mojavensis* in which observed heterozygosity in the different races and subraces ranged from 0.05 to 0.08 (Zouros 1973).

Allele frequencies for *Mdh-1* and *Est-2* in *D. pachea* and *D. nigrospiracula* (not shown) agreed well with values obtained ≈ 30 years ago for the same localities reported here (Rockwood-Sluss *et al*. 1973; Sluss 1975). Thus, allele frequencies seen at these two loci in both species show remarkable temporal stability, even in the highly polymorphic *Est-2* locus of *D. nigrospiracula*. The ecological factors involved in maintaining these polymorphisms over time are unknown. Also, no evidence was found for seasonal changes in allele frequencies in these two species in the earlier studies (Rockwood-Sluss *et al*. 1973; Sluss 1975). The apparent temporal stability in allele frequency, both seasonally and over several decades, is especially interesting given that numbers of adult flies of the three species of *Drosophila* diminish drastically during the summer months, although food resources are available (Rockwood-Sluss *et al*. 1973; Pitnick 1993; Breitmeyer & Markow 1998).

The lack of population structure found for the three species of Sonoran Desert *Drosophila* in our study is consistent with earlier results on *D. pachea* (Rockwood-Sluss *et al*. 1973) and *D. nigrospiracula* (Sluss 1975). Although the number of loci analysed in these previous studies was limited (four and two, respectively), the number of localities sampled was high (11 and 19, respectively). Possible explanations for the lack of population structure seen in desert-adapted *Drosophila* include: (i) frequent remating; (ii) long-distance dispersal; and (iii) their relatively high longevity. For example, females of *D. nigrospiracula* mate up to four times daily, *D. mettleri* females mate twice a day, and those of *D. pachea* mate at least daily (Markow 1996). For two of the desert species, *D. mojavensis* and *D. nigrospiracula*, females have been shown to selectively utilize sperm from genetically unrelated, rather than related, males (Markow 1982, 1997), a phenomenon that would promote outcrossing and heterozygosity. Recent findings from our laboratory reveal that adults of the four desert species are very long lived (T. A. Markow, manuscript in preparation). Average dispersal distances of 100–300 m per day (Table 1), combined with genetically variable sperm loads resulting from multiple matings and a long life-span, could easily result in high gene flow and eliminate any local genetic differentiation. However, once microsatellites are developed for these species, some degree of population structure may be detectable.

Although we found that genetic variability in the three species is not low, our data support the view of Johnston & Heed (1976) that desert *Drosophila* should show little population structure. In contrast, across the same geographical region, *D. pachea* shows significant local differentiation for the 7A and 7+ gene arrangements (Ward *et al*. 1975). Evidence has been presented that variation in karyotype frequencies for this inversion polymorphism is related to the vegetational distribution of different subspecies of the senita host plant (Ward *et al*. 1975; Duncan 1979; Etges *et al*. 1999). A reconciliation between the patterns of population structure based upon allozyme vs. chromosome data may be possible with more detailed molecular genetic approaches. Regardless of whether population genetic data show evidence of differentiation, Markow *et al*. (1983) found no premating isolation among populations of any of these three species from even more distantly located sites than those used here. Thus any differentiation detected with additional genetic studies would not necessarily indicate isolation among populations.

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Therese A. Markow studies ecology and population biology of cactophilic desert-adapted *Drosophila*, with special interests in speciation and the evolution of mating systems. Edward Pfeiler works on developmental physiology and evolution of elopomorph fishes, with special interests in the structure and function of proteoglycans in larval fishes. He also studies Sonoran Desert *Drosophila*, focusing on patterns of allozyme expression during development.
