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# Resistance to thermal stress in desert *Drosophila*

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## Summary

1. Four species of *Drosophila* are endemic to the Sonoran Desert of North America where daily and seasonal high temperatures exceed those experienced by other species in this genus. The close association between these species and their cactus hosts means that they reside only in the desert and raises the question as to whether they are better able to survive heat stress than are non-desert species of *Drosophila*. The tolerance of adult flies of the four desert species *D. mojavensis*, *D. nigrospiracula*, *D. packia* and *D. mettleri* and the cosmopolitan *D. simulans* to acute heat stress was tested.

2. There was considerable variability among the desert endemic species with respect to survival following heat exposure. Two species, *D. mojavensis* and *D. packia*, were more resistant at 44 °C and 46 °C than the others, with *D. mettleri* exhibiting similar heat stress resistance to *D. simulans*.

3. While there was no consistent influence of gender on heat resistance, younger flies (1-day-old) showed significantly greater survival than did older flies (7- or 14-days old).

*Key-words:* Heat, thermotolerance, stress resistance, survival

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## Introduction

Of the 3386 species of Drosophilidae, only four are endemic to the hot Sonoran Desert of North America. These four species, shown in Table 1, feed and breed in the necrotic tissue of specific columnar cactus hosts that are also endemic to the desert (Heed 1978). A number of features of the ecology of these flies have been investigated in order to understand their unique host associations and distributions. These include characterization of cactus chemical composition and microbial communities associated with host necroses (Kircher 1982; Fogleman & Abril 1990), resource quality and availability (Fellows & Heed 1972; Mangan 1982; Etges & Heed 1987; Breitmeyer & Markow 1997), and interspecific competition (Heed & Mangan 1986; Mangan 1982).

The close association with and, in one case, dependence upon specific host plants, exposes desert *Drosophila* not only to unique nutritional and chemical environments, but also, potentially, to temperature extremes not experienced by other species in the genus. Their small size suggests that their body temperatures are isothermal with respect to ambient conditions (Stevenson 1985) and that even with behavioural avoidance of hot microclimates, these flies may risk greater degrees of heat stress than flies of non-desert species at certain times of the day and year.

While the environmental physiology of many desert insects has been intensively studied (Hadley 1994), the physiology of *Drosophila* species other

than *D. melanogaster* has received limited attention. Several lines of evidence suggest that desert *Drosophila* should be able to resist extreme temperatures. First, there appears to be ample genetic variation for heat tolerance in *Drosophila*. Early experiments with *D. melanogaster* showed that laboratory populations respond to artificial selection for heat tolerance (Morrison & Milkman 1978) and rearing populations of this species for several years under different temperature regimes also produced changes in temperature tolerances (Huey, Partridge & Fowler 1991). Isofemale lines (Hogsgood & Parsons 1968) and geographic populations of the same species often exhibit large differences in thermal stress resistance (Parsons 1980; Coyne, Bundgaard & Prout 1983; Krebs & Loeschcke 1995a) as do different species (Yamamoto & Ohba 1984). Second, experiments with *D. buzzatii*, a cactophilic species found in warm habitats, reveal them to be substantially more heat tolerant than *D. melanogaster* (Krebs & Loeschcke 1995a). Finally, the temperature at which synthesis of the heat shock protein, hsp 70, is activated in the desert *D. mojavensis* is considerably higher than for *D. melanogaster* (Huey & Bennett 1990). Although these observations are consistent with the hypothesis that desert *Drosophila* species should be better able to tolerate heat stress than its congeners, this prediction has never been tested.

Below, we present experiments designed to ask if the four desert endemic *Drosophila* exhibit greater resistance to heat stress than other *Drosophila*.

**Table 1.** Sonoran Desert *Drosophila* and their host cactus species

<i>Drosophila</i> species	Host cactus species
<i>D. pachea</i>	<i>Lophocereus schottii</i> (Senita)*
<i>D. mojavensis</i>	<i>Stenocereus thurberi</i> (Organpipe) <i>Stenocereus gummosus</i> (Agria) <i>Ferocactus acanthodes</i> (California Barrel)
<i>D. nigrospiracula</i>	<i>Carnegiea gigantea</i> (Saguaro) <i>Pachycereus pringlei</i> (Cardon)
<i>D. mettleri</i>	Soaked soil of all above species

\*Nutritionally dependent upon host.

Because resistance to high temperatures may be confounded by resistance to desiccation, we selectively examine resistance to high-temperature stress by controlling humidities at saturated levels. Furthermore, different techniques for measuring thermotolerance have been found to measure different and uncorrelated traits (Hoffmann *et al.* 1997), underscoring the importance of selecting a measure that can be compared to other studies. We therefore use the protocol of Krebs & Loeschcke (1994a) from which extensive data on *D. melanogaster* and *D. buzzatii* have already been generated. We also include the cosmopolitan *D. simulans*, the sibling species of *D. melanogaster*, because it is found in urban areas in the Sonoran Desert and because its thermotolerance is reported to be similar to *D. melanogaster* (Parsons 1980; Hoffmann & Watson 1993).

## Methods

### DROSOPHILA STOCKS

All laboratory cultures of flies used were established from multifemale ( $n > 40$ ) wild collections for each species. *Drosophila nigrospiracula* and *D. mettleri* were collected from the Superstition Mountains near Apache Junction, Arizona (33°22'N and 111°22'W), about 50 km (30 miles) east of Phoenix, in December 1994. *Drosophila pachea* and *D. mojavensis* were collected from a site near San Carlos, Sonora, Mexico (27°58'N and 111°05'W) in January 1995. Experiments were performed within several generations of collection.

All flies, except *D. pachea*, were grown on Betty Crocker Potato Buds® (Minneapolis, MN) mixed with yeast. *Drosophila pachea* were grown on Formula 4–24 Instant *Drosophila* Medium (Carolina Biological, Burlington, NC) because this was the only medium in combination with a piece of its host cactus that reliably sustains this species. Media for population bottles consisted of 15 g of media, Carolina or potato flakes, several grams of yeast and 65 ml of water. A piece of autoclaved species-specific cactus tissue was placed in each of the population bottles. Approximately 20 pairs of flies were used to start each bottle and were transferred every 48 h to prevent

larval crowding. Four new bottles were set up every other day to ensure daily emergence of large numbers of healthy flies. When flies began to emerge, bottles were emptied, and collecting began 24 h later. Each collection removed all flies that emerged in the previous 24-h period. Virgin flies were collected and sexed under light CO<sub>2</sub> anaesthesia and placed ( $\approx 20$  per vial) into vials containing banana–agar medium until they reached the desired ages. All flies in population bottles and ageing vials were maintained at 25 °C.

### TESTS FOR THERMOTOLERANCE

To test for thermotolerance in adult flies, a standard protocol was used (Krebs & Loeschcke 1994a,b,c, 1995a,b; Loeschcke, Krebs & Barker 1994) in which individuals were exposed to one of several different test temperatures for 100 min. Survivors were counted 24 h later. Virgin males and females were tested separately at 1, 7 and 14 days after eclosing, resulting in a total of six different sex/age groups. A total of nine vials, each containing 10 flies, were exposed for each sex/age group at each temperature. Exposures for species were performed randomly, depending on ages available at exposure times, for each sex/age group at each temperature.

Immediately prior to testing, flies were transferred from the ageing vials to empty vials so the flies could be counted. Test vials, which contained the banana–agar medium, were placed in the test incubator for a minimum of 30 min (the time required for equilibration) before the actual exposure to stabilize the test condition before flies were introduced. Vials were stoppered with foam plugs saturated with water and inverted to prevent flies from getting stuck in the medium when knocked down by the heat. Humidity was measured at  $> 98\%$ . A Precision Scientific Company Model 4 air incubator (Winchester, VA) was used for all exposures. Temperatures were measured using a mercury thermometer placed on the incubator shelf elevated by foam plugs next to the vial rack. All exposures were for 100 min and test temperatures ranged from 36 to 46 °C (incubator temperature), in 2 degree increments. In-vial temperatures were measured using an Omega 450 ATH digital thermistor thermometer (Stamford, CT) with air probe adapter. After each exposure, flies were transferred to fresh food vials and maintained at 25 °C until scoring. The minimum criterion for survival was appendage movement when prodded with a paintbrush (Loeschcke *et al.* 1994). Survivorship for each vial/replicate was calculated as the proportion of individuals surviving/individuals tested. Data are reported for incubator temperatures.

### STATISTICS

Within each species, mean proportional survival was calculated for sex and age separately at each test

temperature. Inferential statistics were performed using the statistical software SAS (SAS Institute 1989). To stabilize the variances of the proportions, the data were arcsine transformed. Analysis of variance was performed with species and temperature as main effects. Sex and age were nested under species/population and age was nested under sex. Duncan's multiple range tests were performed with  $\alpha = 0.05$ .

### Results

Adult survival following 100-min exposures to high temperatures is presented in Fig. 1(a, b) for the four desert endemics and *D. simulans*. In the interspecific comparison, *D. mojavensis* is represented only by the strain from San Carlos, Sonora. Data from incubator temperatures of 38–46 °C were used in the species, age and sex comparisons. ANOVA (Table 2) revealed that for survival, main effects, nested effects and interactions were statistically significant. Main and nested effects show very clear patterns. One of the desert species, *D. mettleri*, was less heat resistant than the others, being grouped with *D. simulans* at all temperatures by the Duncan's multiple range ( $\alpha = 0.05$ ). Of the remaining three species, *D. mojavensis* was the most tolerant,

with the majority of exposed flies surviving a 44 °C exposure. This temperature clearly separates it from the next most tolerant species, *D. pachea*, in which only a low proportion of flies survive. At the next lowest test temperature, 42 °C, most *D. pachea* but fewer *D. nigrospiracula* live. In summary, the species can be ranked in order of decreasing tolerance to high-temperature exposure such that *D. mojavensis* > *D. pachea* > *D. nigrospiracula* > *D. mettleri* = *D. simulans*.

Sex differences, when they were found, were different for different species, indicating the absence of a general effect of gender on survival. Age, on the other hand, showed a very clear influence on heat resistance, with the younger flies being the most heat tolerant, regardless of species.

### Discussion

The most striking results of this study are the differences in heat tolerance among the desert species and, to a lesser degree, in the greater ability of younger flies of all species to survive heat stress. This discussion will focus first on possible explanations for these species and age differences and then address the implications of the differences for the population biology and ecology of desert *Drosophila*.

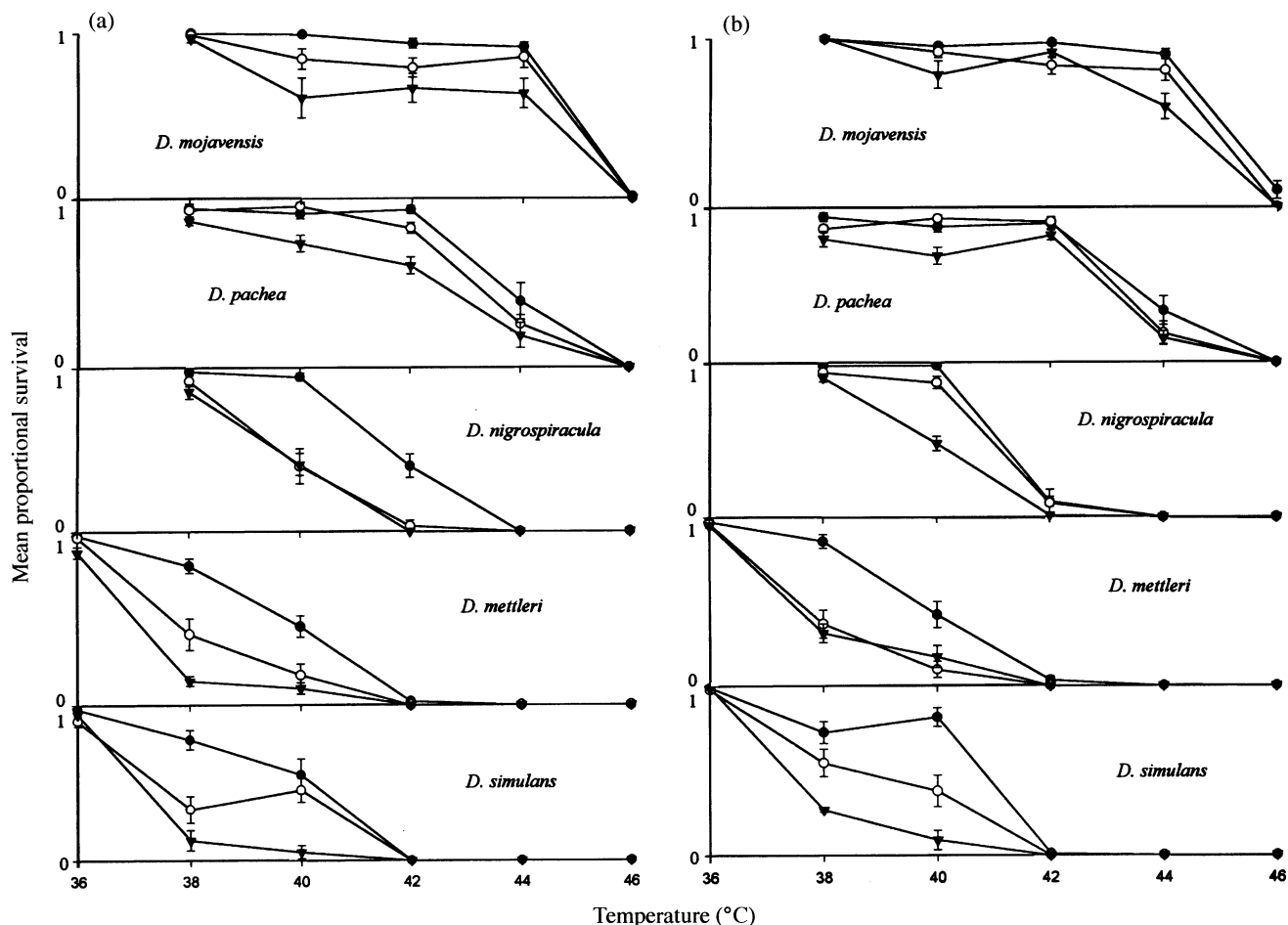


Fig. 1. Mean proportional survival  $\pm$  SE, as a function of test temperature, in Sonoran Desert *Drosophila* (*D. mojavensis*, *D. nigrospiracula*, *D. mettleri* and *D. pachea*) and *D. simulans* at (●) 1, (○) 7, and (▼) 14 days of age: (a) males (b) females.

Interspecific differences of the magnitude observed here were unexpected given the fact that all four desert species live, effectively, side by side in most of their range. The survival differences among desert species are robust with respect to changes in rearing medium and length of laboratory culture. Other experiments in our laboratory (B. Raphael & T. A. Markow, unpublished observation), in which flies were reared on different food and had been in the laboratory for different periods of time prior to testing, yielded comparable survival to the present study. Two species, *D. mojavensis* and *D. pachea*, exhibit markedly higher resistance to short-term heat stress than the other species (Fig. 1). Strains of *D. mojavensis* from other parts of their range, regardless of regional temperature differences, also are highly resistant to acute heat

stress (R. Stratman and T. A. Markow, unpublished observation). Clearly *D. mettleri* is less thermotolerant than the others, but its resistance is not likely to be as poor as for most non-desert species. The apparent similarity of *D. mettleri* to *D. simulans* in the present study may reflect the fact that the *D. simulans* were derived from a collection in Tempe and were more likely to be heat resistant than strains used in previous studies (Parsons 1979).

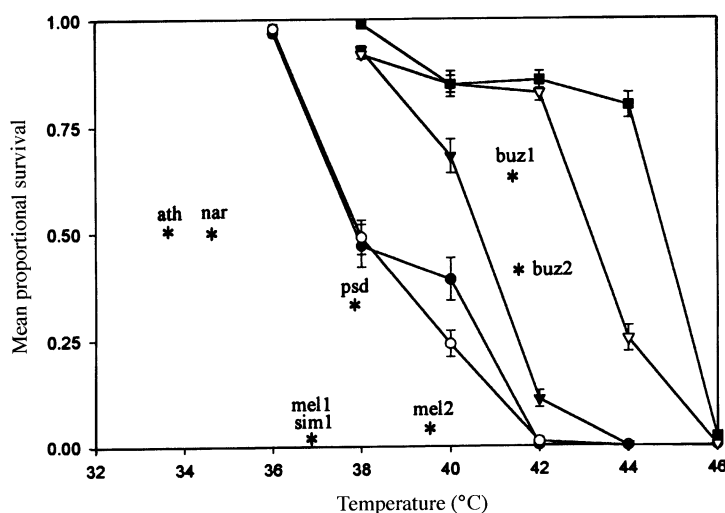
Given the marked variability among the desert species in heat resistance, attempts to evaluate their relative heat resistance should include comparison to as many other species as possible. Unfortunately, heterogeneity in the measures of heat stress resistance limits the number of studies from which meaningful comparative data can be extracted. We have utilized those studies in which comparisons could be made (similar exposure times, temperatures, conditions) and included the relevant points on Fig. 2. Clearly there is overlap between *D. mettleri*, *D. simulans* and *D. melanogaster* although our *D. simulans* exhibited greater heat resistance than those in previous studies. *Drosophila nigrospiracula* and *D. buzzatii*, another cactophilic, repleta group species typically found in warmer localities, are similar in their resistance to thermal stress. Krebs & Loeschcke (1995a) found differences in heat resistance among different geographic strains of *D. buzzatii* and were also able to increase the heat resistance of this species with pretreatment exposure to higher temperatures. Even their most resistant strains and pretreated samples, however, did not exceed the heat tolerances of *D. mojavensis* or *D. pachea*. Thus it appears that the highest thermotolerances reported for *Drosophila* are for desert endemic species, and that as a group, although variable, they are in general more resistant to acute temperature stress than species from other climatic zones.

The differences among the four desert endemic *Drosophila* species are observed despite the fact that all four occupy largely overlapping ranges and are potentially exposed to the same climatic extremes. What accounts for the differences among the desert species? Why are *D. mojavensis* and *D. pachea* superior at surviving acute high-temperature exposures than the others?

Species differences are a function of long-term phylogenetic history, more recent ecological adaptations, and their interaction. In the absence of a phylogenetic study of heat stress resistance, assessment of the role of long-term evolutionary constraints can only be inferential. In addition to any potential phylogenetic constraints, behavioural thermoregulation and host microclimate differences may be effective in mitigating the degree to which each desert *Drosophila* species actually experiences heat stress in nature. That *Drosophila* species exhibit thermal habitat preference differences is well known (Fogleman 1982; Schnebel & Grossfield 1986). In nature, cactophilic *Drosophila* are typically found on

**Table 2.** Analysis of variance of survival for all Sonoran *Drosophila* plus *D. simulans* with species and temperature as main factors. Sex and age are nested within species and age is nested within sex. Survival proportions were arcsine transformed

Source	df	Sums of squares	F-value	P
Temperature	4	188.443	1038.74	0.0001
Species	4	131.126	722.79	0.0001
Sex within species	5	853	3.76	0.022
Age within sex within species	20	20.342	22.43	0.0001
Temperature × species	16	63.030	86.86	0.0001
Temperature × sex	20	2.949	3.25	0.0001
Temperature × age	80	25.380	6.99	0.0001
Error	1188	53.880		



**Fig. 2.** A comparison of mean proportional survival  $\pm$  SE of species in the present study with data obtained from the literature for other species. While the present study employed 100 min temperature exposures, not all previous studies involved identical exposure duration. *Drosophila* species tested in the present study were (■) *D. mojavensis*, (▽) *D. pachea*, (▼) *D. nigrospiracula*, (○) *D. mettleri*, and (●) *D. simulans*. All data points extracted from the literature are designated with a (\*) and a species abbreviation. Buz1 = *D. buzzatii*, 100 min (Krebs and Loeschcke 1995a); buz2 = *D. buzzatii*, 144 min (Loeschcke *et al.* 1994); mel2/sim1 = *D. melanogaster* and *D. simulans*, 6 h (Stanley *et al.* 1980); mel2 = *D. melanogaster*, 90 min (Krebs and Loeschcke 1994a); psd = *D. pseudoobscura*, 35 min (Coyne *et al.* 1983); ath = *D. athabasca*, nar = *D. narragansett*, 100 min (Richmond 1980).

the shady sides of their hosts, although non-desert species have been found to differ considerably in how they change their phototactic behaviour with increasing temperatures (Markow 1979).

The hosts themselves differ dramatically in features that potentially moderate heat stress. These differences include spatial and temporal abundance as well as host size (Breitmeyer & Markow 1997) and water content (Castrezana 1996). When temperatures soar, large cactus (Cardon and Saguaro) arms are expected to retain cooler internal temperatures than smaller ones (Senita and Organpipe) and thus insects occupying their internal crevices would experience different thermal environments. While Feder (1997) reported that larger peaches, exposed to the sun, reach higher internal temperatures than small ones, we expect larger cacti to remain cooler than small ones because the cacti of interest are many times larger than small pieces of fruit (Nobel 1988).

Reduced heat tolerance with age may be a function of senescence; however, the higher thermotolerance of younger flies may also reflect the presence of residual heat shock proteins from earlier developmental stages. Heat shock proteins are not produced only in response to stress. During larval development in *D. melanogaster* hsp synthesis has been detected (Pauli *et al.* 1990). If this is typical of all *Drosophila* species, and if these proteins remain in newly emerged flies, they could protect young adults from thermal stress.

Summer temperatures in the desert exceed those that even *D. mojavensis* was found to tolerate in the present study. Several factors may contribute to the ability of these species to persist in the desert. Our study only examined resistance to acute heat stress in unacclimated flies. Acclimation boosts thermotolerance, and exposure to gradual diurnal cycling in nature is likely to increase the upper limits observed here. There is also reason to believe, from laboratory experiments and from our findings on *D. mojavensis* and *D. simulans*, that *Drosophila* populations can respond rapidly to selection for thermotolerance and may be doing so on a seasonal basis. In addition, life-history stages in *Drosophila* have been found to differ in heat resistance such that the more sedentary stages, eggs and pupae, are more tolerant of high temperatures than are larvae and adults (Krebs & Loeschcke 1995b). Finally, flies may shift to different, and as yet undetected, microhabitats as temperature soar. In summer, populations of all four species undergo an apparent crash, during which adults and larvae are often impossible to find (Rockwood-Sluss, Johnston & Heed 1973; Pitnick 1993; Breitmeyer & Markow 1997), even though necroses are abundant (Breitmeyer & Markow 1997). Clearly we need to know which of the above scenarios accounts for the ability of these four species to live in the desert. Our current research efforts are focused on this question.

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