



# No place to hide: microclimates of Sonoran Desert *Drosophila*

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## Abstract

1. We characterized year-round microclimate conditions (temperature and humidity) in and around necrotic cacti of the Sonoran Desert of southwestern North America. Necrotic cacti serve as host plants for four endemic species of *Drosophila*.
2. Flies in the field were exposed to high and variable temperatures, sometimes ranging between  $<5^{\circ}\text{C}$  to  $>40^{\circ}\text{C}$  in a single 24-h period. Habitat temperatures often exceeded thermal tolerance limits measured in the laboratory.
3. The air inside necroses was more humid than the air outside, but was often warmer during the day than outside air. Thus, air pockets within necroses do not provide a thermal refuge.
4. Necrotic tissues inhabited by *Drosophila* larvae reached temperatures in excess of  $40^{\circ}\text{C}$ , as did the moist soil in which one of the endemic *Drosophila* species undergoes larval and pupal development.
5. We conclude that high temperatures provide a significant environmental stress for Sonoran Desert *Drosophila*, at all developmental stages.

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## 1. Introduction

The extreme temperatures and low humidities of desert habitats provide a severe physiological stress for resident plants and animals. Desert arthropods are particularly vulnerable, because their small size renders them nearly isothermal to the surrounding environment, and their large surface area:volume ratio places them at risk of dehydration. Despite these problems, arthropods

are the dominant animal taxon in deserts around the world.

An important aspect of survival for many desert species is behavioral avoidance of extreme conditions (Bartholomew, 1964). Birds and large mammals may migrate out of the desert during the warmest times of the year, whereas invertebrates and other small animals may retreat to relatively cool, moist microclimates (e.g. burrows) and estivate (Willmer, 1982; Seely, 1989; Cloudsley-Thompson, 1991). Nocturnal or crepuscular activity patterns will also limit exposure to hot, desiccating conditions.

Fruitflies of the genus *Drosophila* occur in a wide range of habitats, including deserts (David et al., 1983). Adults may avoid thermal extremes, presumably by selecting cooler microhabitats (Junge-Berberovic, 1996; Feder et al., 2000), although larvae are less able to avoid

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thermal stress (Feder et al., 1997b). Desiccation and temperature stress can significantly impact *Drosophila* communities, even in mesic environments (Worthen et al., 1998; Worthen and Haney, 1999).

*Drosophila* have invaded the Sonoran Desert of North America on several occasions, resulting in four independently derived extant endemic species: *D. mettleri*, *D. mojavensis*, *D. nigrospiracula* and *D. pachea*. For Desert *Drosophila*, microhabitat selection is likely to be particularly important. Sonoran Desert *Drosophila* can be found at all times of the year, although they are less abundant during the summer than at other times (Breitmeier and Markow, 1998). These species are more tolerant of high temperatures than *D. melanogaster* and other mesic species, suggesting that they are exposed to warmer conditions. Around 50% mortality occurs between 38°C and 45°C for the desert species (Table 1), whereas similar mortality occurs at 36°C or lower in mesic species (Stratman and Markow, 1998; Krebs, 1999). Desert *Drosophila* have higher thresholds for induction of heat-shock proteins (Krebs, 1999) and loss of flight and mating performance (Patton and Krebs, 2001), and are more desiccation-resistant than non-desert species (Gibbs and Markow, 2001; Gibbs and Matzkin, 2001). Sonoran species also differ significantly from each other in thermal tolerance (Stratman and Markow, 1998). For example, *D. mettleri* is less resistant to high temperatures than other species, suggesting that it may experience more benign conditions in nature than other *Drosophila* species.

All four Sonoran endemics are cactophilic, living in the necrotic tissues of damaged columnar cacti (Table 1). These cacti may provide a favorable microenvironment. Temperatures inside rots may be lower than ambient conditions due to shading, and evaporation from necrotic tissues should increase the humidity and reduce water loss from resident flies. However, very high

temperatures have been recorded from the tissues of cacti and other desert plants (e.g. Gates, 1980), so necroses may not be as favorable as one might expect. Species of host cacti may also differ from one another in the microclimates they provide for their resident *Drosophila*, due to differences in morphology (stem and arm diameter; Table 1) that affect cactus temperature.

In this paper, we address several important questions regarding the environmental biology of Desert *Drosophila*. Firstly, do necroses provide relatively cool microhabitats, and do these allow fruitflies to avoid thermal stress? Secondly, are differences in the thermal tolerance of *Drosophila* species related to differences in the microhabitat conditions available in their host cacti? Thirdly, do larval and adult habitats differ in temperature, and are these associated with the thermal tolerances of pre-adult and adult stages? Specifically, we characterized microclimates available to and experienced by larval and adult *Drosophila* in the Sonoran Desert, to help understand how these species survive the harsh environmental conditions typical of deserts.

## 2. Methods and materials

### 2.1. Study sites

We investigated microclimate conditions in three species of columnar cacti that serve as hosts for Sonoran *Drosophila* (Table 1). Necrotic saguaro cacti were studied at several locations in the Tucson, AZ, USA area, including the Arizona-Sonora Desert Museum, Tucson Mountain Park, and local residences. We studied necrotic organ pipe and senita cacti at two sites near San Carlos, Sonora, Mexico (see Breitmeier and Markow (1998) for site descriptions). Most necroses

Table 1  
Characteristics of host cacti studied, and their resident *Drosophila* species

Cactus species	Arm circumference (cm ± SE) <sup>a</sup>	Necrosis size (cm <sup>3</sup> ) <sup>a</sup>	Resident <i>Drosophila</i> species	Thermal tolerance (LT <sub>50</sub> ; °C) <sup>b</sup>
Senita <i>Lophocereus schottii</i>	17.8 ± 7.9	46.5	<i>D. pachea</i>	43
Organ Pipe <i>Stenocereus thurberi</i>	49.6 ± 15.0	24,600	<i>D. mojavensis</i>	45
Saguaro <i>Carnegiea gigantea</i>	113.8 ± 39.9	214,000	<i>D. nigrospiracula</i>	40.5
Moist soil of hosts above	—	—	<i>D. mettleri</i> <sup>c</sup>	38

<sup>a</sup>From Breitmeier and Markow (1998).

<sup>b</sup>From Stratman and Markow (1998).

<sup>c</sup>Larval *D. mettleri* develop in the soil; adults occur in burrows and at necroses of all host species. Larvae of other species develop in necrotic tissues of their host cacti.

form air pockets with an opening to the outside air. Resident *Drosophila* enter through these openings to feed and oviposit. We studied a total of 24 rots, 20 of which had resident populations of adult *Drosophila* at the time of data collection.

## 2.2. Data collection

Environmental conditions were monitored using Hobo dataloggers (Onset Computer Corporation, Bourne, Massachusetts USA), which were placed in potential microhabitats available to Desert *Drosophila*. Temperatures and humidities were recorded at 5-min intervals for periods ranging from 48 h to 13 days. To assess within-host variation, multiple dataloggers were placed in different locations in and around each necrosis.

The Hobo temperature dataloggers (models H8 Temp and H8 Temp/External) had two types of thermistor probes: smaller “internal” probes and larger “external” probes (manufacturer’s terminology). To assess conditions experienced by adult flies, the internal probes were placed in air pockets in necrotic patches, in shaded locations just outside these necroses, and in solar-exposed locations nearby. The internal thermistors were attached to the recorder by a 10-cm wire, and were approximately the same size and color (black) as the Sonoran *Drosophila*. To assess larval habitats, wide-range external thermistors were inserted directly into moist necrotic tissues, or into pools of fluid formed by draining tissues. Under these conditions, both types of sensor had a response time of approximately 1 min.

Humidity dataloggers (model H8 Pro RH/Temperature) were too large to be placed in the smaller pockets typical of senita, and therefore were only placed in large cavities of saguaro and organ pipe rots. These loggers simultaneously recorded air temperatures in the pockets, thus enabling us to calculate the vapor-pressure deficit (VPD, the difference between the saturated water-vapor pressure at a given temperature, and the actual vapor pressure). In some cases, temperature and humidity conditions were measured using a hand-held Omega digital thermohygrometer or digital thermometer (Omega Engineering Inc., Stamford, Connecticut USA).

To investigate microhabitat conditions available for *D. mettleri*, a soil-breeding species that has been observed digging burrows (S. Castrezana, personal communication), we measured temperatures in moist soil saturated with exudate from cactus necroses (where the larvae of *D. mettleri* develop), and in dry soil adjacent to these patches.

## 2.3. Data analysis

We extracted several types of information from our temperature recordings: average, high and low tempera-

tures, and warming and cooling rates. To examine thermal extremes, we first calculated the average temperature for each 1 h period (12 data points collected at 5-min intervals) during a given recording. For each 24-h cycle (midnight to midnight), we then determined the highest mean temperature for a 1 h period. Because the lowest temperatures occurred at night, minimum hourly temperatures were calculated between noon and noon on consecutive days.

To assess rates of thermal change, we calculated the difference in temperature between each pair of measurements taken 60 min apart, for the entire recording period. Maximum heating rates for each 24-h period were determined between midnight and midnight, and maximum cooling rates were calculated between noon and noon on consecutive days.

One of our goals was to assess microclimate variation around individual cacti, so the number of cacti studied was limited by the number of dataloggers available. We studied a total of 24 cacti (six senita, seven organ pipe, and 11 saguaro), with at least one datalogger each deployed in the necrotic tissue, outside air and in the rot pocket. To ease comparisons between microhabitats, data were grouped seasonally, with at least three cacti included in each group. Fall and winter recordings were from October 1999 to March 2000. Because of the limited number of recordings made from senita and organ pipe cacti, we combined data from the spring and summer (April–September) of 1999 and 2000. More recordings were made from saguaro cacti, allowing us to separate data collected in 1999 and 2000.

## 3. Results

Tables 2–4 provide summaries of the microclimate data collected for each host cactus species. In all, over 500 days of temperature data were collected from 133 datalogger deployments at 24 cacti. Approximately 30 days of humidity data were also collected, from four cacti (two organ pipe and two saguaro). Fig. 1 depicts a representative recording from a Hobo temperature logger. Regardless of season, temperatures peaked between 1 and 5 PM, and were lowest around dawn. Not surprisingly, average temperatures were warmer in the spring and summer months (Tables 2–4).

### 3.1. Maximum temperatures

Air temperatures outside necroses frequently exceeded 35°C for all cactus species, and sometimes reached 45°C for brief periods. Maximum 1 h air temperatures were higher in the spring and summer than in fall and winter (e.g. they averaged >40°C vs. 29.6°C, respectively, in Tucson; Tables 2–4).

Table 2  
Temperatures recorded at senita cacti in San Carlos, Sonora

Temperature	Season	Outside air	Air inside pockets	Necrotic tissue
Mean	Fall/winter	17.2 (16.1–18.1)	16.2 (15.2–17.1)	16.7 (15.8–17.6)
	Spring/summer	27.2 (26.5–28.0)	29.1 (27.1–31.0)	29.2 (27.9–31.3)
1-h maximum	Fall/winter	27.7 (26.2–29.0)	30.4 (26.6–34.2)	32.4 (28.2–38.1)
	Spring/summer	40.5 (38.6–42.4)	40.0 (37.3–42.7)	40.2 (37.2–42.0)
1-h minimum	Fall/winter	6.9 (6.1–7.9)	5.9 (5.0–6.9)	6.3 (4.9–7.2)
	Spring/summer	14.0 (13.7–14.8)	20.3 (13.5–27.1)	18.4 (13.8–27.1)

Mean values are provided for  $n=2-8$  recorder deployments (totalling 7–23 days), with the range of values in parentheses. In all, 26 deployments were made for a total of 89 days of recordings.

Table 3  
Temperatures recorded at organ pipe cacti in San Carlos, Sonora

Temperature	Season	Outside air	Air inside pockets	Necrotic tissue
Mean	Fall/winter	19.2 (18.1–20.2)	18.0 (17.3–19.1)	18.7 (17.5–19.8)
	Spring/summer	27.5 (24.1–31.9)	26.6 (22.8–31.5)	28.9 (24.4–33.0)
1-h maximum	Fall/winter	28.0 (25.2–31.0)	26.5 (23.4–33.6)	25.4 (22.1–29.0)
	Spring/summer	36.8 (32.4–42.6)	33.1 (31.4–36.6)	37.7 (34.6–39.2)
1-h minimum	Fall/winter	11.5 (9.8–15.3)	10.4 (8.3–12.1)	11.5 (10.6–12.4)
	Spring/summer	19.8 (14.3–28.1)	18.4 (14.2–28.2)	22.6 (14.9–29.1)

Mean values are provided for  $n=3-7$  recorder deployments (totalling 10–16 days), with the range of values in parentheses. In all, 28 deployments were made for a total of 80 days of recordings.

Air pockets inside necroses were usually slightly cooler than ambient air, but sometimes exceeded 40°C inside saguaro and senita rots. In some rots, internal temperatures were consistently higher than outside. Fig. 2 depicts recordings from a fallen saguaro at the Arizona-Sonora Desert Museum in March 2000. Afternoon air temperatures inside this necrosis were several degrees higher than for shaded air immediately outside the rot. Fig. 3 summarizes temperatures recorded from 22 senita cacti in May 1993, where air temperatures were recorded inside rot pockets and in the shade immediately outside the same necroses. Paired *t*-tests revealed consistently warmer afternoon (1:30–3:30 PM) tempera-

tures inside rots than outside, but no differences in morning (8:30–10:30 AM) temperatures.

For several rots, we deployed multiple dataloggers in similar microhabitats to assess fine-scale variation in climatic conditions. Fig. 4 depicts data from five temperature loggers inside a saguaro rot pocket. At any given time, air temperatures varied by up to 6°C between sites within a given rot, but were usually within 2–3°C of each other.

We also recorded temperatures from the necrotic tissue itself, where larvae of three *Drosophila* species grow and develop (Table 1). For the two smaller host cacti, senita and organ pipe, necroses attained similar

Table 4  
Temperatures recorded at saguaro cacti in Tucson, Arizona

Temperature	Season	Outside air	Air inside pockets	Necrotic tissue
Mean	Spring/summer 1999	34.9 (34.2–36.2)	33.7 (33.2–34.0)	32.8 (29.4–36.2)
	Fall 1999/winter 2000	15.6 (14.0–17.8)	16.6 (13.5–19.6)	16.7 (13.5–20.7)
	Spring/summer 2000	30.2 (24.6–35.7)	28.3 (23.8–32.9)	25.4 (18.5–32.3)
1-h maximum	Spring/summer 1999	44.3 (42.8–46.2)	40.7 (38.0–42.8)	37.9 (33.2–47.2)
	Fall 1999/winter 2000	29.6 (20.0–43.8)	30.8 (22.9–34.8)	25.2 (16.4–34.5)
	Spring/summer 2000	40.6 (35.3–49.8)	36.5 (29.3–45.6)	32.0 (22.7–41.2)
1-h minimum	Spring/summer 1999	26.0 (24.4–27.2)	26.3 (25.4–27.4)	27.3 (24.6–29.6)
	Fall 1999/winter 2000	8.8 (5.8–12.4)	9.0 (6.6–12.3)	11.8 (8.4–17.6)
	Spring/summer 2000	19.5 (11.6–27.2)	19.0 (12.2–25.6)	18.7 (10.6–26.5)

Mean values are provided for  $n=6-15$  recorder deployments (totalling 13–67 days), with the range of values in parentheses. In all, 79 deployments were made for a total of 340 days of recordings.

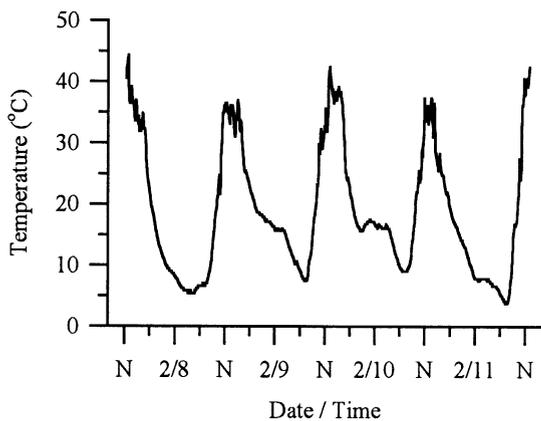


Fig. 1. Recording from a Hobo temperature logger (San Carlos, Sonora, Mexico; February 2000). The thermistor was placed in an air pocket adjacent to necrotic tissue in a rotting senita cactus. “N” indicates noon.

maximum temperatures to the adjacent air (Tables 2, 3), although inspection of recordings revealed a slower rate of temperature increase in the morning. In saguaro, the largest species, tissues heated slowly and usually remained several degrees below air temperatures. Necrosis temperatures between 30°C and 40°C were common in saguaro cacti (Table 4), with maximum 1 h temperatures averaging 35°C in the spring and summer.

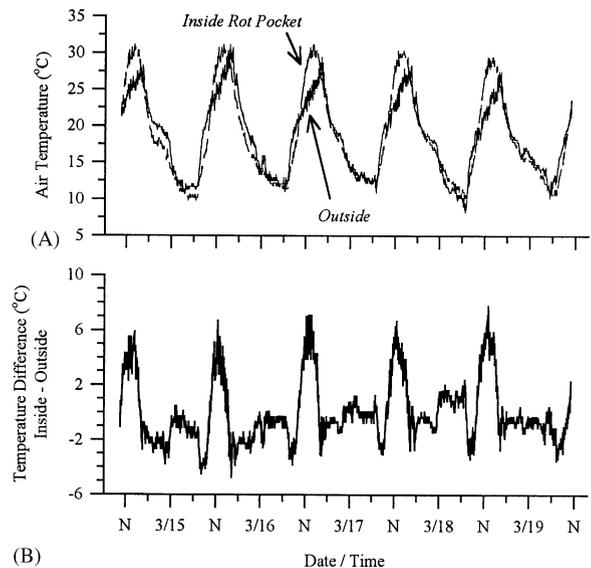


Fig. 2. (A) Air temperatures recorded inside a saguaro rot and immediately outside the same necrosis (Arizona-Sonora Desert Museum; March 2000). (B) Difference between internal and external temperatures, calculated from data in (A). “N” indicates noon.

### 3.2. Minimum temperatures

The lowest absolute temperatures were recorded in November 1999, when ambient temperatures on some

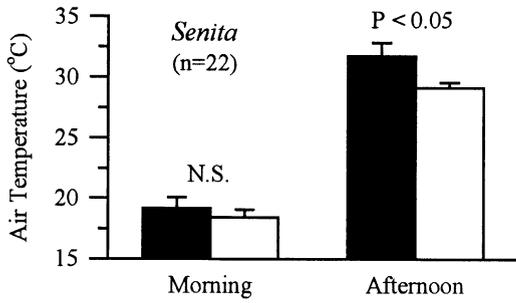


Fig. 3. Air temperatures recorded inside and immediately outside necroses of senita cacti (San Carlos, Sonora, Mexico; May 1993). Filled bars: temperatures in air pockets of necroses; open bars: outside air temperatures for the same necroses. Morning temperatures were measured between 8:30 and 10:30 AM; afternoon temperatures were measured between 1:30 and 3:30 PM. *P*-values were computed from paired *t*-tests.

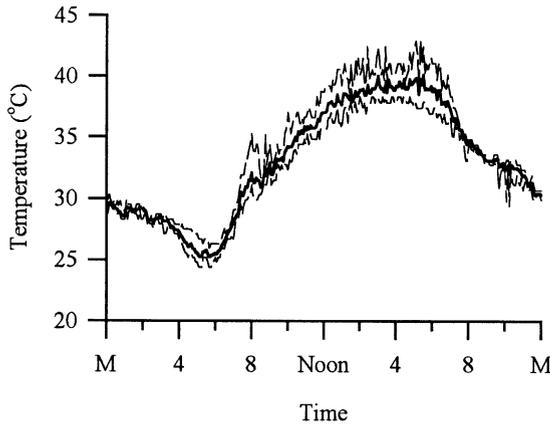


Fig. 4. Temperature variation within a single necrosis. Air temperatures inside a necrotic saguaro were measured using five dataloggers (Tucson, AZ; June 1999). Solid bold line indicates the mean value at each time; fainter dashed lines indicate the maximum and minimum recorded temperatures at each time. “M” indicates midnight.

nights at the San Carlos site nearly reached 0°C. In contrast, outside temperatures near Tucson remained above 25°C between May and July 2000. Minimum temperatures in ambient air and air pockets of necroses were usually within 2–3°C of each other (Tables 2–4).

3.3. Heating and cooling rates

Fig. 5 summarizes data on heating and cooling rates for air and necrotic tissue. The fastest rates of temperature change were observed during the fall and winter, when temperatures often ranged between 5°C and 40°C within a 24-h period. Heating rates up to 20°C/h were recorded for ambient air, but rates of

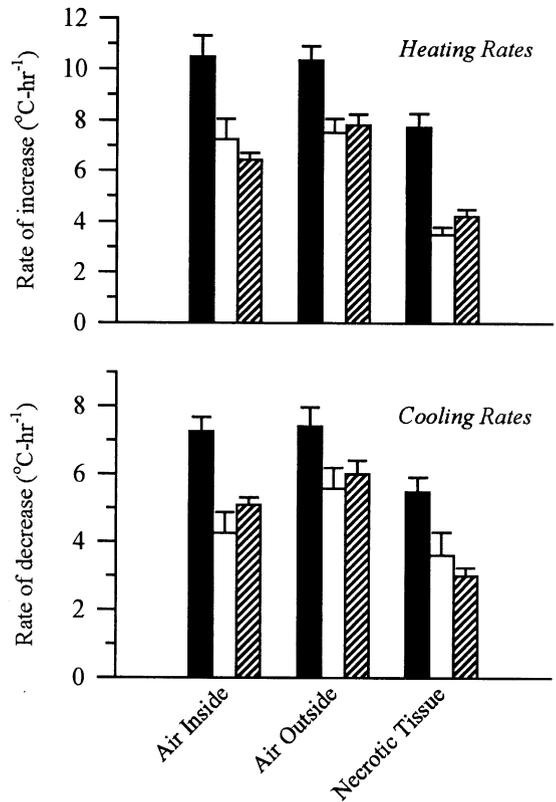


Fig. 5. Heating and cooling rates of *Drosophila* microhabitats. Rates were calculated as the maximum difference between two measurements taken 1 h apart. Bars represent means ( $\pm$  SE) for all recordings. Filled bars, senita; open bars, organ pipe; hatched bars, saguaro.

5–10°C/h were more typical. Cacti cooled ~3°C/h more slowly than they warmed on average (Fig. 5). Similar rates of temperature change were observed for air inside rot pockets and ambient air, while necrotic tissues warmed and cooled more slowly than the air. Senita cacti tended to heat and cool more rapidly than the other, larger host species.

3.4. Humidity

Relative humidities were consistently higher inside cactus rots than outside. They exhibited diurnal cycles in which humidity fell during the day, then increased to ~90% RH at night (Fig. 6). Part of this pattern could be explained by changes in temperature, which is negatively related to relative humidity. However, absolute humidities recorded by the dataloggers exhibited the same patterns. Inside cactus rots, absolute humidities ranged from 5–10 g/m<sup>3</sup> during the day to 15–20 gm/m<sup>3</sup> at night. Outside air cycled diurnally between 2 and 5 g/m<sup>3</sup>.

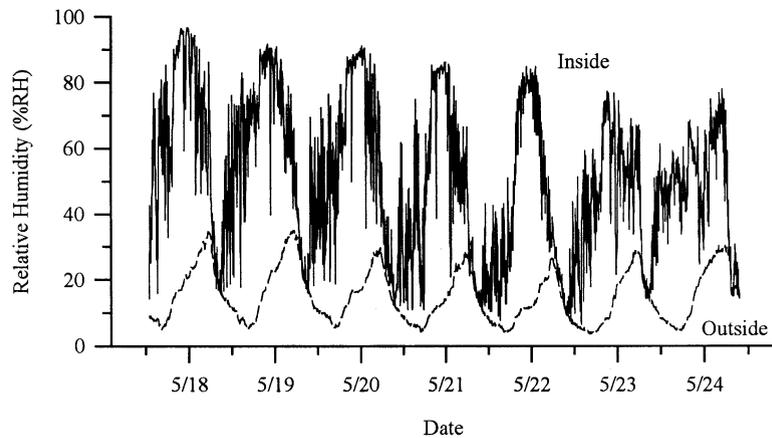


Fig. 6. Recordings of relative humidity inside and outside a saguaro rot (Tucson, AZ; May 2000), recorded using Hobo humidity dataloggers. Upper solid line, internal humidity; lower dashed line, external humidity.

We used our humidity and temperature data to calculate the VPD. VPD provides a measure of the gradient for water flux through the insect cuticle; the greater the VPD, the more desiccating the air (Hadley, 1994). VPDs above 12 kPa were frequently recorded outside rots in the afternoon, but typically remained below 5 kPa inside rot pockets (not shown).

### 3.5. Soil temperatures

Fig. 7 depicts 1 h maximum temperatures recorded from damp soil, where *D. mettleri* oviposits and develops, and adjacent dry soil. Soil surface temperatures often exceeded 50°C, and dry soil could reach >40°C at depths of 1–2 cm. Moist soil, and pools of liquid formed by particularly large necroses, usually remained below 35°C, even when ambient air temperatures exceeded 40°C. Moist and dry soils had similar minimum temperatures.

## 4. Discussion

Surprisingly little is known about the environmental conditions actually experienced by immatures or adults of any *Drosophila* species in nature. Temperature and humidity affect the structure of *Drosophila* communities (Worthen et al., 1998; Worthen and Haney, 1999), suggesting that microclimate variation is an important ecological factor. Jones et al. (1987) used a strain with a temperature-sensitive eye-color mutation to show that *D. melanogaster* in the field (eastern United States) develop at an average of 21°C, whereas more recent experiments reveal that developing larvae may be subjected to high or lethal temperatures in some locations (Feder et al., 1997b). Other studies suggest

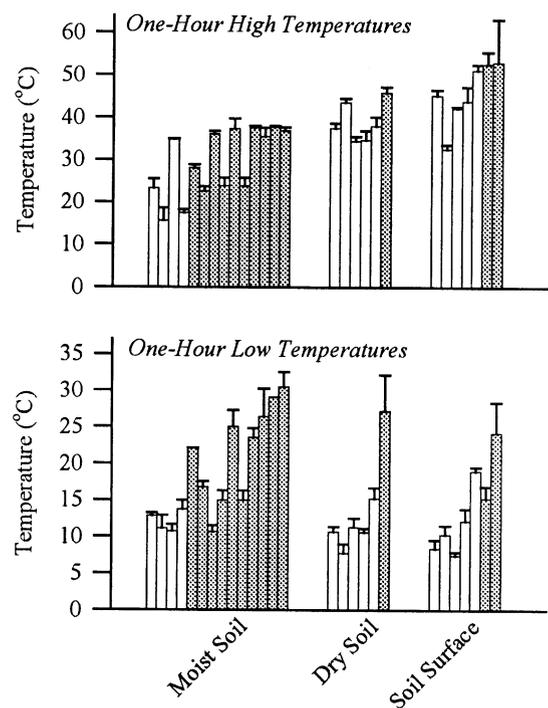


Fig. 7. Maximum and minimum 1-h temperatures recorded in potential habitat for larval *Drosophila mettleri*. Open bars, fall and winter temperatures; filled bars, spring and summer temperatures. Data are means  $\pm$  SE for 3–7 days.

that adult *D. melanogaster* behaviorally avoid thermal extremes (Junge-Berberovic, 1996; Feder et al., 2000).

In this study, we tested the hypothesis that necrotic cacti provide cool, relatively benign microhabitats that allow Desert *Drosophila* to avoid thermal stress. Although populations of Sonoran Desert *Drosophila* decline in warmer months (Breitmeyer and Markow,

1998), flies were present at 20 of the 24 rots we studied, even in the summer. Whenever possible, we placed our thermistors right where we saw flies. We did not routinely check for the presence of larvae, but we did observe them in a few rots. It is likely that, if adults are present, larvae are as well (W. B. Heed, personal communication). *Drosophila melanogaster* will lay eggs in fruit that has previously been heated to lethal temperatures (Feder et al., 1997a), indicating that female flies do not avoid excessively warm oviposition sites. If Desert *Drosophila* follow the same pattern, then larvae were presumably present in most of our necroses. In summary, we feel we were able to obtain an accurate depiction of the conditions experienced by Desert *Drosophila* in nature at all developmental stages.

#### 4.1. Microhabitats of adult *Drosophila*

Air pockets of necrotic cacti do not appear to provide a refuge from extreme temperatures, suggesting that thermal stress is unavoidable for Sonoran Desert *Drosophila* (Tables 2–4). Indeed, temperatures inside these pockets were often warmer than the surrounding air (Figs. 2,3), with temperatures in and near senita and saguaro rots sometimes exceeding 42°C. Thus, opportunities for behavioral thermoregulation by site selection appear to be limited.

An important issue is whether our measurements of environmental temperatures accurately reflect body temperatures of *Drosophila* in the field (Bakken, 1992). Some insects reduce their heat load by reflecting a large portion of the solar radiation (McClain et al., 1991; Jacobs and Watt, 1994), or by evaporative cooling (Toolson, 1987). These mechanisms are unlikely, however, to affect *Drosophila* body temperatures significantly, because the utility of both mechanisms is dependent on body size. Insects below 3 mg, including all four species of Sonoran *Drosophila*, are isothermal to air even when placed in direct sunlight (Willmer and Unwin, 1981), and the lower size limit for effective evaporative cooling is ~100 mg (Prange, 1996). Thus, our measurements of air temperatures where flies actually occur provide an accurate indication of the body temperatures experienced by Desert *Drosophila*.

Not surprisingly, Sonoran *Drosophila* are more resistant to thermal stress than *D. simulans* and other mesic fruitflies (Stratman and Markow, 1998). Nonetheless, the heat tolerance of a Desert *Drosophila* species does not appear to predict which cacti it occupies. For example, *D. mojavensis*, the most thermally tolerant fruitfly (Stratman and Markow, 1998), occurs in organ pipe cacti in Sonora, which had the lowest observed thermal maxima of the three host species (Table 3). One might expect that *D. mettleri*, which occurs on or near the ground at all of the host cacti, to be as resistant as the other species, yet it is the least tolerant species.

Although necroses do not provide a refuge from ambient temperatures, they do provide the advantage of higher humidities than the outside air. An unanticipated finding was that relative humidities inside air pockets were often significantly below 100% RH and varied diurnally due to changes in both temperature and the absolute water content of the air (Fig. 6). Because these spaces are enclosed and the necrotic tissues are very moist, we had expected to find higher, more constant RH values. A potential contributing factor is the large size of the humidity probes used (~8 cm in diameter and ~5 cm tall for the RH datalogger). Thus, only larger necroses could be examined, and the opening to the rot pocket sometimes needed to be enlarged so that the probe could be inserted. Although we minimized our manipulations and used duct tape to cover most of the openings, these rots may have had greater movement of air between the pocket and the outside than other necroses, which would lower the internal RH values. However, even if our selection was biased to more open, less humid rots, rot pockets are clearly much more humid than the outside air.

A less well-studied aspect of *Drosophila* thermal biology is the effect of cold temperatures. The lowest temperatures we recorded were just above freezing at the San Carlos site, although frosts occur several times each winter in the Tucson area. Several *Drosophila* species, including *D. nigrospiracula*, are able to survive 24 h or more at temperatures below 0°C (Lowe et al., 1967; Yamamoto and Ohba, 1984; Hori and Kimura, 1998; Kely and Lee, 1999). If this is true for the other Sonoran endemics, then winter low temperatures may not be an important environmental factor affecting fruitfly survival.

#### 4.2. Microhabitats of *Drosophila* larvae

Necrotic tissues, where larvae of three Sonoran *Drosophila* species develop, had extreme temperatures similar to those of the surrounding air. Because plant tissues have a higher heat capacity, necroses heated more slowly than air, but senita and organ pipe rots attained maximal temperatures similar to those of the surroundings. Thermal maxima of saguaros were >5°C lower than those of ambient air (mean values of 35°C vs. 42°C in the warmer months; Table 4), due to their much larger size and thermal inertia compared to the other cacti, but temperatures above 39°C were recorded from necroses of all host species.

Little is known about the thermal tolerance of Desert *Drosophila* larvae. Larval *D. mojavensis* begin to express heat-shock protein 70 at 39°C and exhibit high mortality above 42°C (Krebs, 1999). Other Sonoran *Drosophila*, as pupae, are less tolerant of thermal stress (Markow and Stratman, 2002). Thus, our data suggest that high temperatures may cause significant pre-adult mortality

in nature, as has been demonstrated for *D. melanogaster* in orchards (Feder et al., 1997b).

Burrows are much cooler and more humid than ambient air during the day, and provide a classic example of a favorable microhabitat for desert invertebrates (Willmer, 1982; Cloudsley-Thompson, 1991). Only one of the Sonoran species, *D. mettleri*, is known to use burrows (S. Castrezana, personal communication), and it also oviposits and develops in moist soil below necroses. At 1 cm in depth, moist soil remained up to 20°C cooler during the day than nearby dry soil (Fig. 7), presumably due to greater heat capacity and evaporative cooling, although soil temperatures occasionally approached 40°C. Temperatures rarely dropped below 10°C, so that soil conditions were much less variable than air or rot temperatures. At greater depths in the soil, diurnal variation would be even less. It is interesting to note that *D. mettleri* is the least heat-tolerant of the Sonoran *Drosophila* (Table 1). Recall, however, that adults can also be collected at necroses, and thus can be exposed to the same high temperatures as the other three *Drosophila* species.

#### 4.3. Implications for the ecology of Desert *Drosophila*

Our findings present a severe challenge to our understanding of the ecology of Desert *Drosophila*. Although necroses provide abundant water and a humid atmosphere, all developmental stages may be exposed to temperatures above 40°C for one to several hours, sufficient to cause high mortality under laboratory conditions (Krebs, 1999). Survival is not the only issue. At 38–39°C, flight performance and mating success are severely compromised (Patton and Krebs, 2001). How do Desert *Drosophila* persist in such a warm habitat? Although pupae and larvae clearly cannot escape thermal stress, adults may make significant use of other, as yet unknown, microhabitats. Sonoran *Drosophila* are generally considered to exhibit strong host preferences (Fellows and Heed, 1972; Lofdahl, 1985; Etges et al., 1999), but observations of milkweed polenia on adult *D. nigrospiracula* (Polak and Markow, 1998) and stable-isotope data from field-collected adult *D. mojavensis* and *D. pachea* (Markow et al., 2000) indicate that these species use food sources other than cacti. Even if flies spend a significant amount of time at other plants, however, it seems unlikely that temperatures there would be any lower than around cacti.

The most likely refuges from heat and desiccation would be underground. Only *D. mettleri* is known to enter or dig burrows, but whether other Sonoran Desert *Drosophila* do as well should be investigated more closely. Burrow use might explain the near absence of all species except *D. nigrospiracula* at some times in the summer. Alternatively, Desert *Drosophila* may migrate to other areas or to higher elevations. This possibility

has not been examined very thoroughly, although long-distance migrations have been reported for other *Drosophila* species under desert conditions (Coyne et al., 1982). One final possibility is that, although the temperatures we measured are high enough to kill non-acclimated *Drosophila* in the laboratory, they may increase at rates that allow flies time to synthesize heat-shock proteins or to acclimatize in other ways. Temperatures usually increased or decreased at 5–10°C/h (Fig. 5), rates that extend the thermal tolerance range of *D. melanogaster* at both high and low temperatures (Feder et al., 1997b; Kelty and Lee 1999, 2001).

In summary, we can reject the hypothesis that Desert *Drosophila* can avoid extreme conditions by inhabiting necrotic cacti. Indeed, necroses are sometimes even more extreme, and *Drosophila* appear to experience harsher physical conditions, particularly in the summer, than they can survive in the laboratory. To solve this conundrum, we need more information on the time budgets of Desert *Drosophila*, to understand the thermal regimes they actually experience in nature, and laboratory experiments are needed that better mimic conditions in the field.

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