

EFFECTS OF TEMPERATURE ON BEHAVIOR OF *TRIMEROTROPIS PALLIDIPENNIS* (ORTHOPTERA, ACRIDIDAE)

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ABSTRACT—We observed activity and behavior of *Trimerotropis pallidipennis* in the field and constructed time-activity budgets during June–July 2003. Grasshoppers began to walk once site temperatures (shaded air temperature 1 cm above soil surface) reached 18.6°C, foraging began once temperatures reached 24.2–31.7°C, and courtship began once temperatures reached 30.3–36.4°C. Mating and oviposition occurred when temperatures reached 30–40°C. Quiescence occurred most often at the lowest and highest site temperature categories (20–25, 25–30, and 45–50°C), and the highest frequency of foraging occurred most often at temperatures of 35–40°C. We observed no clear diurnal patterns for walking in grasshoppers, and found no significant difference between frequency of activities in morning and evening, within the same temperature ranges. Males rested, courted, and groomed significantly more frequently than females, and females foraged significantly more than males. Activity patterns, especially quiescence and foraging, were influenced much more by environmental temperature than by time of day.

RESUMEN—Observamos la actividad y el comportamiento de *Trimerotropis pallidipennis* en el campo durante junio y julio del 2003. Utilizamos estos datos para hacer presupuestos de tiempo-actividades. Los saltamontes empezaron a caminar cuando la temperatura del sitio alcanzó 18.6°C (la temperatura del aire en la sombra 1 cm sobre el suelo), empezaron a forrajear cuando la temperatura alcanzó entre los 24.2 y 31.7°C y empezaron a cortejar cuando la temperatura alcanzó entre los 30.3 y 36.4°C. El apareamiento y la ovoposición ocurrieron cuando la temperatura alcanzó entre los 30 y 40°C. El descanso ocurrió más en la primera y última categoría de temperaturas (20–25°C, 25–30°C y 45–50°C) y el forrajeo ocurrió más entre 35 a 40°C. No observamos un patrón diurno claro para el caminar de los saltamontes, y no encontramos diferencias significativas entre la frecuencia de las actividades en la mañana y la tarde, dentro de la misma categoría de temperaturas. Los machos descansaron, cortejaron, y se acicalaron significativamente más que las hembras, y las hembras forrajearon significativamente más que los machos. Los patrones de actividad, especialmente las actividades de descanso y forrajeo, fueron influidos mucho más por la temperatura que por la hora del día.

Body temperature of insects affects all aspects of their lives including metabolism, locomotor performance, feeding rates, digestion, reproductive activities, and developmental rates. These factors, in turn, affect insect populations and their involvement in community and ecosystem processes (Kingsolver, 1989; Toolson, 1998). Distributions of animals at the global scale and microsite selection at the local scale determine thermal opportunities and limitations that constrain performance of most ectotherms. Our overall objective was to understand how high environmental temperatures constrain the behavior and activity of *Trimerotropis pallidipennis*.

Trimerotropis pallidipennis (Burmeister) is a common grasshopper in western North America,

ranging from southwestern Canada to Argentina (R. E. Pfadt, <http://www.sdvc.uwyo.edu/grasshopper/fieldgde.htm>). This species occurs in habitats that range from desert lowlands with elevations of 30 m to forest rangelands as high as 2,590 m (Barnes, 1960). Although it can be found throughout a range of habitat types, it primarily occupies deserts that consist of dry, open areas and sparse grasslands where it feeds on a variety of forbs and grasses (Otte, 1981), spending most of its time on the soil surface (Chappell, 1983; Wallner, 1987). Because *T. pallidipennis* preferentially occupies dry, open areas with little vegetation and spends its time on the ground, individuals are exposed to conditions where environmental and body tempera-

tures potentially exceed lethal maximum temperatures for many hours of each day during spring and summer. Although many studies have examined effects of temperature on activities of insects by quantifying activity as a function of air temperature (shaded air temperature 1 m above the substrate; Uvarov, 1977; Joern et al., 1986; Whitman, 1988; Harrison and Fewell, 1995; Lock and Durwael, 1999), we focused on environmental air temperatures near the substrate (within 1 cm) where these animals reside.

With these data, we hoped to gain insight into how closely coupled activities of this animal were to air temperatures within their habitat. Goals of this study were to: 1) quantify activity budgets of *T. pallidipennis* as a function of site temperature and time of day; 2) determine if sexes differ in activity budgets; and 3) produce an assay of behaviors engaged in by this species.

MATERIALS AND METHODS—Study Site—We conducted our study 18 June–23 July 2003 at the Sevilleta National Wildlife Refuge, Socorro Co., New Mexico. The study site was a plains-mesa grassland at an elevation of 1,670 m, dominated by blue grama grass (*Bouteloua gracilis*), with black grama grass (*B. eriopoda*) and galleta grass (*Hilaria jamesii*) and occasional low-lying forbs and cacti (*Opuntia*). The perennial short-grass to mid-grass species grow sparsely, with pale-colored sandy substrate exposed between grass clumps (ground cover was about 16%). Meteorological data were provided by a Sevilleta Long Term Ecological Research, remote-automated, weather station, located ≤ 30 m of the study site.

Activity Budgets—We arbitrarily selected 86 adult *T. pallidipennis* for observation and attempted to observe each individual for 90 min. We recorded total duration of each activity to the nearest second. Activities recorded fell into four categories: 1) quiescence, 2) walking (walking on substrate or crawling on vegetation), 3) foraging (active tasting and eating), and 4) other (all other activities: courting, mating, grooming, leg and wing movement, flying, crouching).

We measured shaded air temperature 1 cm above the soil surface (hereafter, site temperature) at an arbitrarily selected location ≤ 60 –90 cm from the individual being observed, using an 26-ga Omega copper constantan thermocouple and an Omega HH2002AL hand-held digital thermometer (Omega Engineering, Inc., Stamford, Connecticut). Because we hoped to gain insight into how these grasshoppers respond to changes in air temperatures within their habitat, all site temperatures we measured were from sites on open, unshaded ground between vegetation. These areas represent foraging areas occupied by *T. pallidipennis*, i.e., areas that they preferentially occupy unless the temperature in these areas exceeds or falls below those that allow normal activity. To avoid disturbing grasshoppers, we did not place the thermocouple ≤ 60 cm from the animal. Because of uniformity

of the habitat, it is reasonable to expect that the site temperature measured would match the site temperature around the grasshopper. Site temperature was taken at the beginning of the observation period and about every 15 min thereafter, unless weather conditions changed radically and warranted more frequent temperature measurements. We also recorded general weather conditions for the day, as well as time of sunrise and sunset.

RESULTS—Mean maximum air temperature (at 1 m) at this site for June and July was 34.7°C, mean minimum temperature was 19.1°C; with maximum highs and lows of 41°C at 1500 h and 12.6°C at 0600 h. Mean wind speed (at 3 m) was 4.7 m/s, with a maximum of 24 m/s. Precipitation was 11.5 mm in June and 4.2 mm in July. Sunrise and sunset occurred at about 0700 and 2020 h Mountain Standard Time.

We observed a total of 86 individuals, but omitted data from 14 individuals because they were observed during periods with high winds (≥ 11 m/s), rain, or cloud cover. We also did not use observations of one pair of individuals mating and one female ovipositing in our analyses because these behaviors did not reflect the general daily behavior patterns of most of the population. We calculated activity budgets from 69 individuals (38 females, 27 males, 4 sex unknown) that were observed on days with windspeeds ≤ 6 m/s. Observation periods ranged from 10 to 143 min, with an average of 72 min, and total observation time for the 69 individuals was 78 h. We observed individuals only during periods of sufficient sunlight (0618–2135 h). Using these data, we constructed two activity budgets; frequency of behaviors as a function of time of day in 1-h increments (Fig. 1), and frequency of behaviors as a function of site temperature in 5°C increments (Fig. 2).

Microhabitat Selection and General Survey of Behavior—Before sunrise, individual grasshoppers tended to occupy microsites on the ground, close to edges of grass clumps, resting largely immobile with abdomens pressed directly onto the substrate. At these times, they were reluctant to move or fly if disturbed. We did not find any individuals that were sitting in grass clumps or up on vegetation before sunrise.

Shortly after sunrise, individuals shifted orientation of their bodies so that they were perpendicular to incoming solar beams, but continued to press their abdomens to the soil. Grasshop-

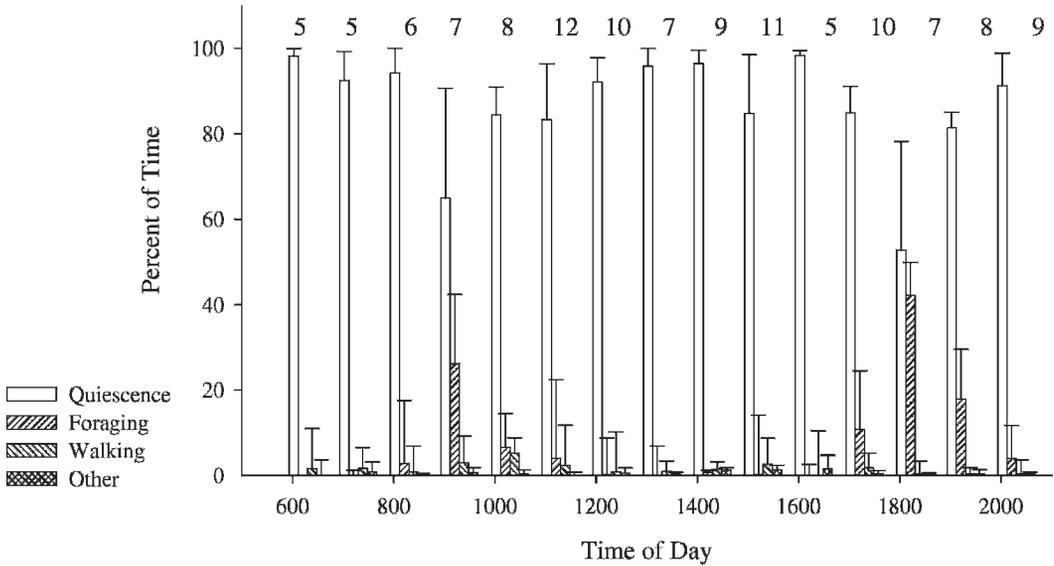


FIG. 1.—Medians and upper 75th percentiles of activity frequencies of *Trimerotropis pallidipennis* throughout the day. Sample sizes for each time category are shown at the top of the graph.

pers did not appear to move into areas where they were exposed to sunlight at dawn. Individuals were either in areas that were in sunlight once the sun rose, or waited 15–50 min after dawn to move into sunlit areas. Activities such as foraging and courtship commenced 0800–0900 h (Fig. 1), and continued throughout the morning.

As the day warmed, grasshoppers increasingly adopted thermoregulatory postures and orientated to reduce heat loads. These behaviors included positioning their bodies so that they were directly facing the sun, stilting, and raising their wings while lowering their abdomens away from their wings to increase convective heat loss. During the hottest part of the day, many individuals occupied cooler microsites higher on vegetation with their heads directly facing the sun. These sites on vegetation were 3–20 cm above the soil surface on grass and forb clumps and stalks and as high as 1 m when resting on cacti. After 1600 h, as temperatures were decreasing, individuals descended from vegetation and frequency of walking, courting and ground foraging increased. Near sunset, we observed the same behaviors, including orienting perpendicular to solar beams and pressing their abdomens into the ground, as in the morning. Our observations indicate that foraging and walking continued after sunset, and that individuals

remained on the ground in the open or under grass clumps.

Foraging Behavior—Grasshoppers typically foraged on the open ground between clumps of vegetation and appeared to spend much of their time consuming detritus (45% of the time). They also fed on both live and dead grasses and forbs. Foraging occurred most often during mid-morning and in early evening (0900–1000 h, 26% median of total activity time; 1800–1900 h, 42%; Fig. 1). Foraging essentially was suspended during mid-day when grasshoppers moved off the substrate into cooler microsites in vegetation.

Reproductive Behavior—Reproductive activity was not common enough to warrant an activity category of its own. However, we observed instances of courtship (stridulation, femur tipping) both within our study species and with other species at the study site. We observed two failed mating attempts, which occurred at site temperatures of 38.6 and 39°C. In both instances, the male approached a female who was resting on open substrate, and as he approached he performed femur tipping. The female performed femur tipping in response. The male then hopped on to the back of the female, who remained motionless, and hopped off again after about 40 s. We observed one instance of successful mating at a site temperature of 36.2°C. The male and female already were coupled in a side-

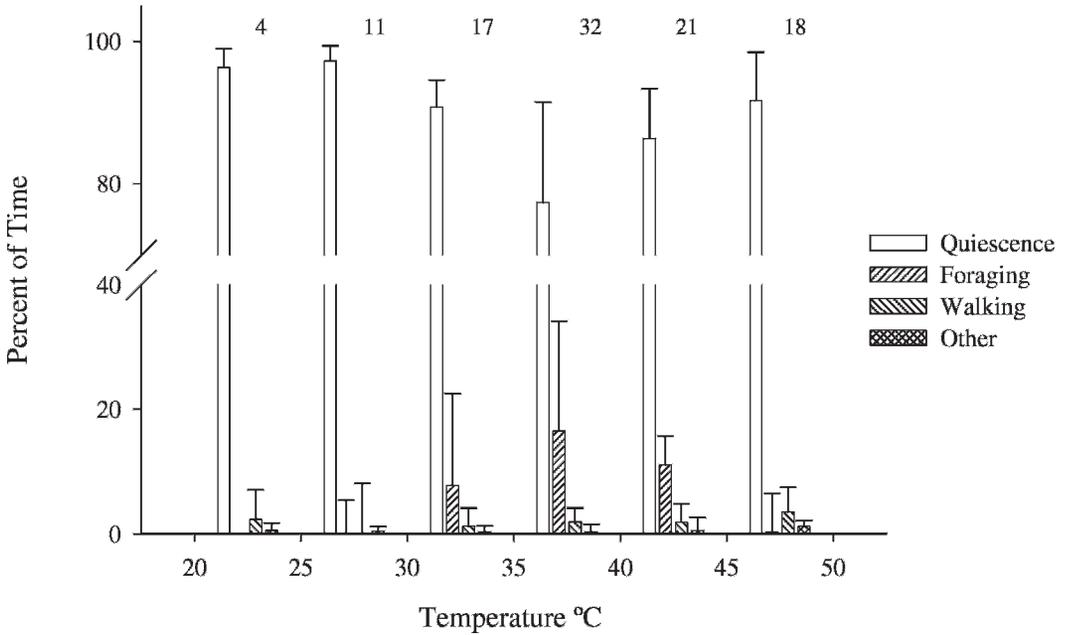


FIG. 2—Medians and upper 75th percentiles of activity frequencies of *Trimerotropis pallidipennis* in relation to shaded air temperatures 1 cm above the soil surface. Sample sizes for each category are shown at the top of the graph.

by-side orientation when the observer approached. After 15 min, the couple shifted to a male-on-top-of-female orientation. Mating continued for 44 min from the time of the approach of the observer to uncoupling of the male and female. We also observed one occurrence of oviposition, which occurred at site temperatures between 30.3 and 36.4°C and in full sunlight. This female initially was resting on open substrate and then began testing the ground with the tip of her abdomen. She dug five holes by positioning her abdomen perpendicular to the ground and using the tip to push dirt away; two initial superficial holes (≤ 0.25 cm), two deep holes the length of her abdomen, and a final hole in the dirt pile from a newly excavated burrow, where she oviposited. Oviposition lasted 57 min from the time when she began digging the final hole until she withdrew her abdomen and covered the hole by kicking dirt over it with her back legs. We did not observe any males that appeared to be mate-guarding.

Temperature Dependence of Behavior—There was no significant effect of time of day on behavior when data were corrected for site temperature (Kruskal-Wallis non-parametric test of medians: quiescence, $P = 0.15$; foraging, $P = 0.16$;

walking, $P = 0.13$; other, $P = 0.37$). Using 5°C intervals for site temperature, we calculated frequency of behaviors as a function of site temperature. Categories for which we had data for ≤ 4 individuals were not included in the analysis. Within the study period, site temperature ranged from 18.6 to 50.7°C ($36.7 \pm 8.10^\circ\text{C}$, mean \pm SE). We observed quiescence most often at lowest (20–25°C) and highest temperature (45–50°C) ranges, during which time individuals were almost exclusively engaged in postural and positional thermoregulatory behavior (Fig. 2). We observed grasshoppers walking when site temperature reached 18.6°C; animals walked throughout the day as individuals searched for thermally suitable microsites, courted, and foraged. Foraging commenced when site temperatures reached 24.2–31.7°C, and increased in frequency with site temperature until a peak frequency of 17% of their total time between 35 and 40°C. At site temperatures $\geq 40^\circ\text{C}$, foraging frequency decreased to 11% at 40–45°C, and 0.3% at 45–50°C. All grasshoppers observed were on open ground in full sunlight at site temperatures ranging from 20 to 30°C. Between 30 and 35°C, 58% of individuals remained on open ground, while the others moved between open

ground, partial shade, full shade, and up onto vegetation. Between 35 and 40°C, only 21% of individuals remained exclusively on open ground in full sunlight. Above 40°C, all individuals were either up on vegetation, in partial shade, in full shade, or moved between combinations of the three microhabitats and occasionally open ground. We observed no individual that remained exclusively on the ground in full sun during the hottest part of the day (>40°C).

Temperature-dependent Behavioral Differences—Males spent significantly more time resting, courting, and grooming than females over all temperature categories (Kruskal-Wallis tests: resting; $P = 0.01$, courting $P = 0.01$, grooming $P = 0.04$). Females spent significantly more time foraging than males over all temperature categories (Kruskal-Wallis test of foraging, $P = 0.001$).

DISCUSSION—Thermoregulatory Strategy—One of the main challenges posed to grasshoppers inhabiting desert environments is avoidance of extreme environmental temperatures, particularly extreme high temperatures. Exposure to high environmental temperatures can cause body temperatures to reach values that induce locomotor dysfunction, paralysis, and death (Parker, 1982; Chappell, 1983). To limit their exposure to high temperatures during the hottest part of the day, grasshoppers often select cool microsites (May, 1979). However, this requirement to occupy cooler microsites may interfere with foraging by forcing individuals out of preferred feeding sites (Uvarov, 1977). For example, individuals that prefer to feed up on vegetation may be forced down into shaded sites to reduce solar-heat loads when air temperatures are high at mid-day, which results in a decrease in feeding rates (Chapman, 1959).

In a study of *T. pallidipennis* at low elevation, Chappell (1983) noted that surface temperatures of soil at his site reached highs between 60 to 70°C and body temperatures sometimes reached 49.3°C. Maximum allowable body temperature is 52°C in this population. To avoid overheating, individuals spent most of the day crouched under shade and partial shade provided by vegetation. In contrast, for our study, we determined that temperatures 1 cm above the soil surface rarely exceeded 50°C and individual body temperatures never exceeded 45.9°C. Our population of *T. pallidipennis* showed a different

thermoregulatory strategy, and climbed onto vegetation to avoid high temperatures. This movement up onto vegetation provided a wider range of air temperatures than those encountered on the substrate. For example, air temperatures at microsites 3–6 cm above the substrate were 2.3–2.9°C lower than those of air temperatures on the substrate. At 50 cm above the substrate, temperature was 10.9°C lower than that of the substrate. At 1 m above the substrate (on cacti), we recorded temperatures 7.1–10.5°C lower than at the soil surface. These more-pronounced thermoregulatory movements also come with a cost because the preferred foraging substrate for this species is on the soil surface. Although some individuals at our site did take advantage of partially and fully shaded microhabitats on the ground, available shade was limited by sparse vegetation and did not allow for continued foraging during hottest parts of the day. In contrast, grasshoppers studied by Chappell (1983) only occasionally took advantage of readily available elevated microsites. Assuming that the population examined by Chappell (1983) also fed on detritus, remaining on the soil surface under vegetation with access to detritus may have allowed them to continue foraging during the hottest part of the day.

Differences Between Sexes—Females spent significantly more time foraging than males. This may be attributed to larger body size of females and their need to acquire a greater amount of energy for oogenesis. Energetic demands of reproduction on males seemed to be limited to energy invested in courtship and sperm production, and appeared to be relatively low. Although males courted both females and other males by walking toward prospective mates and femur tipping, frequency of walking in males was not significantly different from that of females. It is possible that males show increased energetic demands later in the season when they increase their searching activities.

Activity Budgets—Our study site provided an ideal opportunity to investigate how closely behavior is tied to local thermal conditions. The open habitat and almost constant sun provide little shade, which forces grasshoppers to use behavior to minimize exposure to solar-heat loads when temperatures are high. We fully understand that the environmental heat loads that animals experience in nature are an

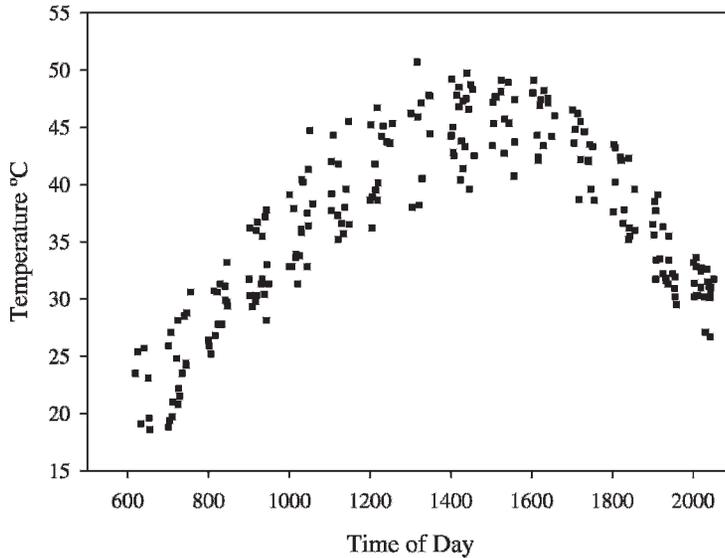


FIG. 3—Shaded air temperature at 1 cm above the soil surface on unshaded open ground between vegetation as a function of time of day throughout the study period ($n = 247$).

integration of radiative, convective, and conductive heat exchange. Thus, we use temperature simply as a minimum index of environmental temperature of the preferred habitat of *T. pallidipennis*.

Frequencies of behaviors, particularly foraging and quiescence, showed a more distinct pattern when analyzed as a function of temperature, rather than of time of day, and highlight the dominance of the thermal environment as the primary driver of behavior in ectotherms. Our study was conducted over a period of about 5 weeks; temperatures recorded at a given time of day varied throughout the study period (Fig. 3). Because of this variability, we were able to disentangle the relative influences of time-of-day and air temperature on behavior of our population. We also found that this species spends much of its time quiescent, and although this behavior can be explained in large part by thermal constraints, likely is driven by other factors such as risk of predation. Chambers et al. (1996) reported that in two species of *Schistocerca*, a large proportion of time spent in quiescence was due both to restricted polyphagy, which resulted in long bouts of feeding from one source, and the risk of predation for cryptic species, for which movement may increase predation. Both of these explanations apply to *T. pallidipennis*, which prefers detritus and whose

cryptic color patterns match those of the substrate.

Conclusions—This study demonstrates the importance of quantifying features of the thermal environment when studying behavior of ectotherms. If activities of ectotherms were quantified simply as a function of time of day, this type of activity budget would not take into account the influence of daily variations in abiotic influences and seasonal effects. A study based on time of day would lack important context and could lead to flawed conclusions about factors that drive activity.

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