

Metabolism and Thermoregulation in Desert and Montane Grasshoppers*

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Abstract. Temperature regulation and oxygen consumption were examined in two species of grasshoppers: *Melanoplus sanguinipes* from cold alpine tundra at elevation 3,800 m, and *Trimerotropis pallidipennis* from hot desert habitats at elevation 250 m. Both species utilized behavioral thermoregulation to keep body temperature (T_b) more constant than environmental temperatures (T_e) during the day. The difference in average T_b in the two species was much less than the difference in T_e 's. Microclimate measurements indicate that temperature regulation is not difficult for *M. sanguinipes*, but *T. pallidipennis* must restrict activity for much of the day to avoid heat stress and can easily overheat if it moves into sunlit areas. Oxygen consumption ($\dot{V}O_2$) at average T_b and total daily energy expenditures are higher in *M. sanguinipes* than in *T. pallidipennis*, as is the Q_{10} for $\dot{V}O_2$. These differences may be related to different strategies for energy utilization and predator avoidance.

Introduction

Insects from a variety of taxa control body temperature by behavioral means (see review by Casey 1981). The mechanisms and effectiveness of temperature regulation in locusts and grasshoppers (Orthoptera: Acrididae) are of special interest because of the diversity of habitats (from low deserts to arctic and alpine tundra) occupied by this group. Heat production and heat balance during locust flight were examined by Weis-Fogh (1956), and behavioral thermoregulation in several grasshoppers and locusts has been observed in both field and laboratory (Uvarov 1977). However, there have been relatively few studies that attempted to correlate the degree of thermoregulation with the microclimate conditions available to the animals. It is well known that major environmental parameters such as wind and solar radiation strongly affect the "temperature excess" (body temperature – air temperature) attainable by insects (Digby 1955, Church 1960a, b). The structure and complexity of microhabitats is also important. For example, a careful study by Anderson et al. (1979) demonstrated that in some grasshoppers behavioral thermoregulation

is precluded by thermal homogeneity within the preferred habitat.

Because of these factors, one might expect that grasshoppers from contrasting thermal environments might show correlated differences in behavioral thermoregulation. Changes in metabolic rate, and its relationship to body temperature (the familiar van't Hoff or Q_{10} effect), might also occur. I examined these possibilities by comparing microclimates, body temperatures, behavior, and energy metabolism in two California grasshopper species, *Melanoplus sanguinipes* from cold alpine tundra and *Trimerotropis pallidipennis* from hot desert habitats.

Materials and Methods

Field Sites. *Melanoplus sanguinipes* were observed in an alpine meadow at 3,800 m elevation near the University of California's Barcroft Laboratory in the White Mountains of eastern California. Terrain consisted of talus fields interspersed with short-grass meadows on a slight east-facing slope several hundred meters above treeline. Vegetation consisted almost exclusively of perennial grass tussocks. Ground cover was approximately 40% during the study period (late August, 1981).

Trimerotropis pallidipennis were investigated on a gently sloping alluvial fan at the University of California's Deep Canyon Research Station in the Coachella Valley of southern California. This area (elevation 250 m) was covered with typical Colorado Desert vegetation, including cacti, xeric-adapted perennial shrubs, and spring annuals. At the time of the study (early August, 1981) most of the annuals had disappeared and ground cover was approximately 15%.

Body Temperatures. Grasshopper body temperatures (T_b) were measured with a probe consisting of a 0.03 mm diameter copper-constantan thermocouple threaded into a 27- or 30-gauge hypodermic needle. The needle was attached to a 1 ml syringe filled with wax, and connected to a thermocouple thermometer (Bailey BAT-12) resolving 0.1° C (calibrated against an accurate mercury thermometer). Grasshoppers were captured with an insect net or gloved hand, and the probe was quickly inserted at least 5 mm into the thorax to obtain T_b . Measurements were made within 3–6 sec of capture. Air and soil surface temperatures (T_a and T_g) at the capture site were also recorded.

Whenever possible, I observed the behavior and microhabitat position of grasshoppers for ~1 min prior to

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capture. However, in many cases I did not notice the animals until they were frightened into escape behavior (leaping or short flights). When this happened I immediately captured the insects (usually within 10–15 sec), obtained T_b , and measured T_a and T_g at the site where the animals had been resting.

Oxygen consumption. I measured the energy metabolism of grasshoppers as oxygen consumption ($\dot{V}O_2$) at several ambient temperatures. Metabolism chambers consisted of 60 ml plastic syringes equipped with 2-way stopcock valves. Animals were placed individually into syringes (with open valves) and allowed to adjust to the experimental temperature for 40–60 min. To begin a measurement, the metabolism syringes (along with one or two syringes of reference air) were flushed with ambient air by 10–15 cycles of rapid filling and emptying to 75–80% of capacity (without crushing the grasshoppers). Assuming complete mixing in the syringes, the proportion of residual air was approximately 10^{-6} . Stopcock valves were then closed, and the syringes were held for 15–65 min at the desired temperature. At the end of metabolism runs, sample and reference gases were injected at constant pressure and flowrate through dessicant (Dryerite) into an Applied Electrochemistry S-3A oxygen analyzer. The $\dot{V}O_2$ was calculated by multiplying the volume of the syringe by the change in oxygen concentration and dividing by the run time, after converting volume to STPD. Atmospheric pressure was obtained from a mercury barometer. The respiratory quotient (RQ) was assumed to be 1.0, since the animals fed primarily on carbohydrates and were not starved prior to the experiments ($\dot{V}O_2$ measurements were always made within 4 h of capture). In no case did oxygen concentration fall below 19.8% during a run.

Following $\dot{V}O_2$ determinations, *T. pallidipennis* were killed with ethyl acetate vapor and weighed to the nearest milligram (mg) on a Sartorius balance. No balance was available at the Barcroft field station, so *M. sanguinipes* were killed, dried, and later weighed to the nearest 0.1 mg on a Mettler balance in my laboratory at the University of California, Riverside. Dry mass was converted to wet mass by dividing by 0.34. This factor (range 0.31–0.40) was determined by comparing wet to dry mass in 15 *M. sanguinipes* transported alive to Riverside.

Microclimate Data. I utilized the operative environmental temperature (T_e , Bakken 1976) as the principal thermal index in grasshopper microhabitats. The T_e is the equilibrium temperature which a metabolically inert body with the size, shape, color, and surface characteristics of the animal in question will attain in specified conditions of T_a , wind speed (V), and solar radiation. Body temperatures of non-flying grasshoppers closely approximate T_e , since metabolic heat production and evaporative heat loss are very small compared to heat exchange by conduction, convection, and radiation (Anderson et al. 1979).

Field measurements of T_e were made using dried grasshoppers equipped with 40-gauge thermocouples and placed in normal postures in natural microhabitats. Dried grasshoppers have the same size, shape, and color as live animals and hence react similarly to T_a , V , and radiation (Bakken 1976). Two to three such ' T_e thermometers' were placed in each microhabitat of interest; a 40-gauge thermocouple within 2–4 cm of each dried grasshopper measured T_a .

Wind speed was determined with hot-bead anemometers placed within 15 cm of dried grasshoppers. Anemometers consisted of pairs of polished aluminum spheres 13 mm in diameter, one of which was heated a known amount through an embedded electrical resistor. The resulting temperature difference was inversely proportional to wind speed (Chappell and Bartholomew 1981). Solar radiation was measured with a LiCor LI-185 radiometer and LI-200S sensor. Microclimate variables were recorded continuously on a 24-channel multipoint recorder or every 15 min on a microprocessor-based datalogger system.

Results

Activity and Behavior. Both *Melanoplus sanguinipes* from Barcroft and *Trimerotropis pallidipennis* from Deep Canyon were active primarily during the day. Only a few individuals were captured before sunrise or after sunset, despite considerable searching. Within h after sunrise, however, grasshoppers could be found in large numbers (*M. sanguinipes* in particular was extremely abundant). In early to mid-morning, both species frequented open, sunlit areas. By 09.00–10.00 h, most of the *T. pallidipennis* had moved from bare ground and were located in the shade under shrubs or occasionally in patches of grass. In contrast, *M. sanguinipes* remained in exposed areas throughout the day.

Behavioral responses to environmental temperature by grasshoppers include several well-defined postures (Waloff 1963, Anderson et al. 1979). Typically, if grasshoppers are exposed to strong sunlight, the extension of the legs increases as temperatures increase, such that cold animals crouch with bodies held against the substrate (if it is warm), while hot animals 'stilt' with the body held as high above the substrate as possible. Both *M. sanguinipes* and *T. pallidipennis* used the full range of these postures when artificially heated or shaded. However, when observed in the field, *M. sanguinipes* were mostly found in a crouched posture, except in the midafternoon on hot days. In contrast, *T. pallidipennis* were usually stilted, except in the early morning when air and ground temperatures were low.

For most of the day, I saw little evidence of orientation with respect to the sun's position in either species (except for shade-seeking in hot conditions). Some basking behavior was observed for *M. sanguinipes* early in the morning. The animals would sit quietly in the sun with their long axis perpendicular to the solar beam. When shaded from direct sunlight and illuminated with sunlight reflected from a mirror, they would reorient to the reflected beam, "tracking" it as it was moved about. Most basking behavior ceased within an hour or two after sunrise.

Body Temperatures. Insect body temperatures may change rapidly during intense muscular activity, as occurs when netted animals struggle to escape. To avoid this possibility I measured T_b within a few seconds of capture. On several occasions I obtained T_b immediately after capture, allowed the animal to struggle for 20–30 sec, and repeated the T_b measurement. In no case did T_b change by more than 1° C between readings, and in 7 instances out of 12 the change was less than 0.5° C.

After the sun had risen, both *M. sanguinipes* and *T. pallidipennis* had T_b 's hotter than the air temperature at the capture site (Fig. 1), but temperature excess ($T_b - T_a$) tended to decrease as T_a increased. Slopes of the regressions of

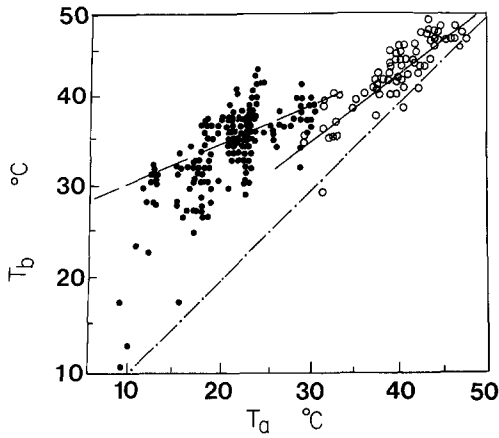


Fig. 1. Relationship between body temperature (T_b) and air temperature at the site of capture (T_a) in wild *Trimerotropis pallidipennis* (open circles) in Deep Canyon (elevation 250 m) and *Melanoplus sanguinipes* (dark circles) at Barcroft (elevation 3,800 m). Dashed and dotted line represents $T_b = T_a$, solid line is regression of T_b on T_a for *T. pallidipennis*, and dashed line is the similar regression for *M. sanguinipes*

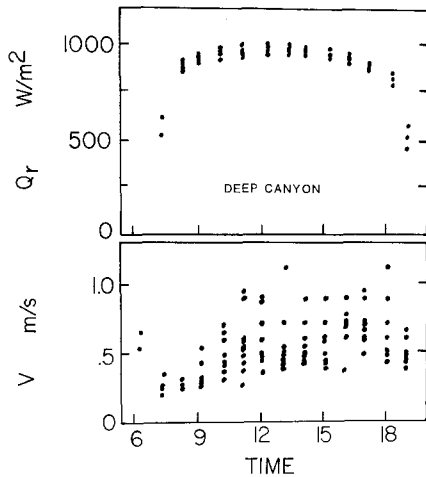


Fig. 2. Incident solar radiation (Q_r , top) and wind speed (V , bottom) at the Deep Canyon site. Wind speed measured 1 cm above soil surface

T_b on T_a were significantly different from 0 and 1 for both species. However, the slope for *T. pallidipennis* (0.75 , $r^2 = 0.761$, $N = 77$) was significantly greater ($P < 0.01$) than the slope for *M. sanguinipes* (0.54 , $r^2 = 0.408$, $N = 200$), indicating that T_b is more highly dependent on T_a in *T. pallidipennis*. Temperature excess in *M. sanguinipes* was usually much larger than for *T. pallidipennis* (about 15°C as opposed to 5°C), and the range of T_b 's in *M. sanguinipes* (32.7°C) was considerably greater than observed for *T. pallidipennis* (19.6°C). Nevertheless, the average T_b 's of the two grasshoppers were fairly similar (35.3°C for *M. sanguinipes* and 43.0°C for *T. pallidipennis*; $N = 200$ and 77 respectively), despite large differences in environmental conditions. The maximum T_b observed for *M. sanguinipes*, 43.4°C , was only 5.9°C cooler than the maximum of 49.3 for *T. pallidipennis*.

Microclimates. During the study periods, the weather at both field sites consisted of clear, sunny days with moderate winds (Figs. 2 and 3). Solar radiation intensity was 10–15%

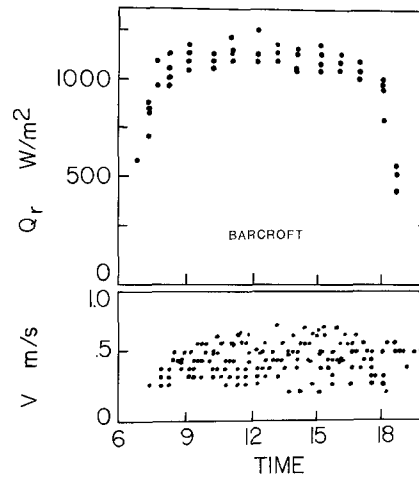


Fig. 3. Incident solar radiation (Q_r , top) and wind speed (V , bottom) at the Barcroft site. Wind speed measured 1 cm above soil surface

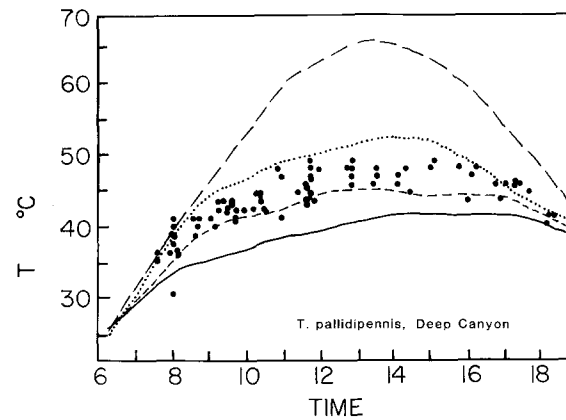


Fig. 4. Environmental (T_a) and body temperatures for *Trimerotropis pallidipennis* at Deep Canyon. Solid line: T_e for grasshopper in deep shade under large, dense shrubs. Short dashes: T_e for grasshoppers in the shade of *Encelia* and *Larrea* shrubs. Dotted line: T_e for grasshoppers in "stilted" posture in open areas. Long dashes: T_e for grasshoppers in crouched posture in open areas. Dots represent body temperatures of free-living grasshoppers

higher at Barcroft, presumably because of the more transparent atmosphere at high altitudes, and wind speed at grasshopper height (1 cm) was lower at Barcroft. Nevertheless, air, ground, and grasshopper environmental temperatures (T_e) were 15 – 20°C hotter throughout the day at Deep Canyon than at Barcroft. Figures 4 and 5 show grasshopper T_e in some of the microhabitats used by the animals, ranging from the coldest (shade) to the hottest available (on the soil surface in full sunlight). The body temperatures of field-caught grasshoppers are also shown.

Metabolism. Energy metabolism measured as oxygen consumption increased as T_a increased for both *Melanoplus sanguinipes* and *Trimerotropis pallidipennis*. Body temperature was not measured during these experiments, but in no case was metabolic heat production large enough to generate a temperature gradient of more than 0.3°C between T_b and T_a (calculated from unpublished data on thermal conductance). I therefore assumed T_b was equal to T_a . The $\dot{V}\text{O}_2$ was expressed in units of watts/g or $\text{cc O}_2/\text{g}\cdot\text{h}$ to facili-

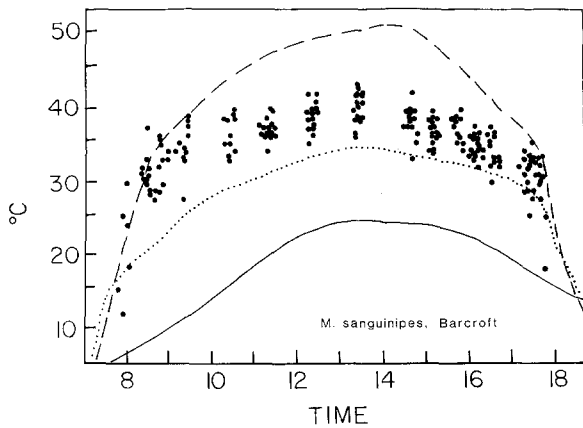


Fig. 5. Environmental and body temperatures for *Melanoplus sanguinipes* at Barcroft. Symbols as in Fig. 4 except that solid line represents T_b in shade of grass tussocks

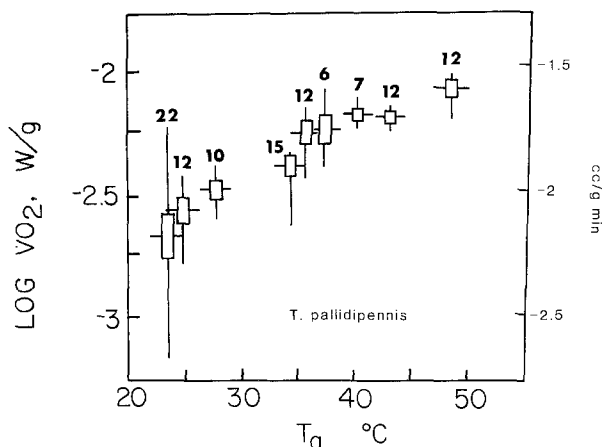


Fig. 6. Oxygen consumption ($\dot{V}O_2$) as a function of temperature (T_a) in *Trimerotropis pallidipennis*. Vertical line is range, horizontal line is mean, and bar is 2 standard errors on either side of the mean

tate interspecific comparisons, although mean body masses were similar (328 mg for *T. pallidipennis* and 295 mg for *M. sanguinipes*).

A plot of $\log \dot{V}O_2$ against T_a is approximately linear for both species (Figs. 6 and 7). For *T. pallidipennis*, the data are adequately described by the regression $\log \dot{V}O_2$ (watts/g) = $0.0234(T_a) - 3.15$ ($r^2 = 0.69$, $N = 108$). The low r^2 value is due mainly to the high variability at $T_a = 23.5^\circ\text{C}$ (Fig. 6). Nevertheless, the slope is significantly different from zero ($P < 0.05$). The Q_{10} for $\dot{V}O_2$ is 1.72 in *T. pallidipennis*, or about 70% of the "normal" value of 2.5. Some leveling off of the Q_{10} curve occurred at temperatures above 38°C , but the slope of the regression of $\dot{V}O_2$ on T_a for T_a below 37°C ($Q_{10} = 1.89$) is not significantly different from the slope for T_a of 38°C and above ($Q_{10} = 1.40$).

The fit of the $\dot{V}O_2$ data to a straight line is very close for *M. sanguinipes* at T_a between 12 and 35°C : $\log \dot{V}O_2 = 0.0426(T_a) - 3.389$ ($r^2 = 0.915$, $N = 48$). At $T_a = 42.5^\circ\text{C}$ (the highest temperature used for this species), $\dot{V}O_2$ appears to be slightly depressed (Fig. 7). If the 42.5°C data are included, the regression becomes $\log \dot{V}O_2 = 0.0348(T_a) - 3.238$ ($r^2 = 0.90$, $N = 60$). Both of these regressions have

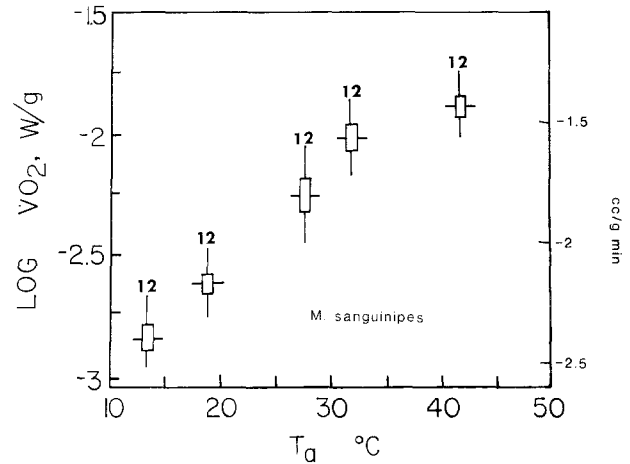


Fig. 7. Oxygen consumption as a function of temperature in *Melanoplus sanguinipes*. Symbols as in Fig. 6

slopes significantly greater ($P < 0.01$) than the slope of the similar regression for *T. pallidipennis*. The Q_{10} value for *M. sanguinipes* is 2.67 at T_a between 12 and 35°C , dropping to 2.23 if all data points are included.

Discussion

Temperature Regulation and Microclimates. Examination of Fig. 1 suggests that *Trimerotropis pallidipennis* from Deep Canyon are less effective thermoregulators than are *Melanoplus sanguinipes* from Barcroft. The slope of the regression of T_b on T_a is significantly higher in *T. pallidipennis*, indicating that T_b is more highly dependent on T_a in this species. *T. pallidipennis* T_b 's are within about $5\text{--}7^\circ\text{C}$ of T_a throughout the day, while *M. sanguinipes* maintain a "temperature excess" of $\sim 15^\circ\text{C}$. However, both grasshoppers show postural responses appropriate for behavioral thermoregulation (Waloff 1963, Anderson et al. 1979) when subjected to hot and cold conditions in the laboratory, and both environments offer enough heterogeneity so that the animals can select from a variety of thermal regimes. Also, the T_b 's of wild-caught *T. pallidipennis* average only 7.7°C higher than those of *M. sanguinipes*, despite microclimate temperatures at least 20°C higher in Deep Canyon than at Barcroft.

Both *T. pallidipennis* and *M. sanguinipes* succeed in maintaining T_b more constant than environmental temperatures throughout the day, but the major thermoregulatory "problems" of the two species are quite different. At the high-altitude Barcroft site, T_a and T_g drop to 0°C or below at night, and even after the sun rises near-ground T_a increases slowly to a maximum of about $25\text{--}30^\circ\text{C}$. Thus the principal thermoregulatory challenge for *M. sanguinipes* is to keep T_b high in the face of low T_a . The animals accomplish this task by maximizing exposure to solar radiation through early morning basking behavior, and by avoiding shaded areas throughout the remainder of the day. The necessity of utilizing open habitats is indicated by the data in Fig. 5. Almost all *M. sanguinipes* T_b measurements throughout the day fell between the T_e 's for animals crouched against the soil surface (the hottest microclimate), or 'stilted' to an height of 1 cm above the soil in sunlight. Several T_b 's in the early morning were higher than the soil

surface temperatures I measured, probably indicating that the animals were better at finding the warmest microenvironments than I was. In contrast, shade T_e 's during the day were cooler than T_b by at least 10° C (by up to 20° C in the morning). Thus, in order to maintain a high and relatively constant T_b , *M. sanguinipes* need simply remain in sunlit areas and adjust its degree of stiling above the substrate. Overheating is essentially impossible for this species. Although ground temperatures occasionally exceed 50° C, the T_e for 'stilted' grasshoppers is always 10–15° C cooler (well within the observed T_b range). All animals observed on bare ground at midday were stilted. When foraging in grass clumps, *M. sanguinipes* showed very little behavior that was obviously thermally related, except to move into the sunlight if they were artificially shaded.

Unlike *M. sanguinipes*, *T. pallidipennis* must continually strive to keep T_b as low as possible. Except for a short period after sunrise, thermal conditions for grasshoppers in open areas are intolerably hot in Deep Canyon. The upper limit of T_b for this species is about 52° C; some locomotory dysfunction begins at T_b 's above 50° C and the grasshoppers attempt to avoid temperatures above 46–47° C (unpublished observations). Ground temperatures exceed 50° C by 09.00–10.00 and attain levels of 60–70° C for several hours, with T_e 's for stilted animals remaining between 45 and 50° C for most of the day. In general, thermally acceptable conditions for *T. pallidipennis* dependably occur only in shaded microhabitats (Fig. 4). As might be expected, after about 09.00 most individuals were found on the ground under *Larrea* or *Encelia* plants; occasionally they ascended a few cm into the branches. The steeper slope of the T_b - T_a regression in *T. pallidipennis* probably reflects the lack of cool refugia in its desert habitat. At high T_a the animals have moved into the coolest available microclimate and have no further ability to reduce T_b ; hence, T_b will closely track shade T_a .

Field observations revealed that *T. pallidipennis* spent much more of their time engaged in thermoregulatory behavior than did *M. sanguinipes*, despite the greater independence of T_b from T_a in the latter species. When resting during the hot parts of the day, *T. pallidipennis* positioned themselves in the small patches of shade cast by leaves or branches, continually "tracking" them as the sun moved. Unless the animals were disturbed, little or no additional activity was noted. This observation contrasts somewhat with that of Anderson et al. (1979), who found that greater development of thermoregulatory behavior was associated with greater independence of T_b from T_a in two species of grasshoppers from Colorado grasslands.

Despite the shade-seeking behavior of *T. pallidipennis*, average T_b during the day was 43° C and several individuals had T_b 's within 1 or 2° C of the upper limit of 50° C (T_b exceeded T_a under shrubs because shade was usually partial and soil temperatures were normally 5–10° C above T_a). These high T_b 's may limit the duration and effectiveness of escape behavior. Frightened *T. pallidipennis* typically fly for short distances (3–10 m), land, and freeze into immobility in a crouched posture. Flights usually terminate on bare, shadeless ground. A grasshopper with a T_b of 43–44° C which lands on 65° C soil can sit for less than a minute before T_b approaches 50° C (unpublished observations). At this point the animal must move into the shade (thereby giving away its position), or risk death from hyperthermia.

Metabolism. The oxygen consumption of both *Melanoplus sanguinipes* and *Trimerotropis pallidipennis* at body temperatures of 20° C is within the range of $\dot{V}O_2$ measured in other resting insects (Batholomew 1981). However, The Q_{10} for $\dot{V}O_2$ in *T. pallidipennis* (1.72) is significantly lower than that of *M. sanguinipes* (2.23), and is also substantially less than the normal value of 2–2.5 (Bartholomew 1977). The observed Q_{10} 's are probably realistic for free-living grasshoppers, since all $\dot{V}O_2$ measurements for *T. pallidipennis* and *M. sanguinipes* were made at temperatures regularly experienced by the animals in the field.

Differences in Q_{10} are reflected in absolute rates of energy metabolism. At the average daytime T_b 's experienced by the two species, $\dot{V}O_2$ is about 50% higher in *M. sanguinipes* than in *T. pallidipennis* (42 J/h vs 28.5 J/h respectively). If Q_{10} -determined $\dot{V}O_2$ is integrated over average T_b during a typical day, total daily metabolic expenditures for *M. sanguinipes* (~550 J) are 27% higher than for *T. pallidipennis* (~435 J). The temporal patterns of energy expenditure are also different. *M. sanguinipes* spends only 9% of its daily energy budget during the 12 h of night and approximately $1/2$ –1 h of morning warm-up and evening cool-down. Low nocturnal metabolism results from low temperatures (0–5° C) at night and *M. sanguinipes*'s high Q_{10} . In contrast, *T. pallidipennis* has a low Q_{10} and experiences nighttime temperatures of 20–25° C. Consequently, this species spends about 35% of its daily energy budget during the night, morning warm-up, and evening cool-down.

Ecological considerations may help explain the differences in metabolic rate and Q_{10} in the two grasshoppers. At the high-altitude Barcroft site, the snow-free activity season for grasshoppers lasts only 3–4 months, but during this period food supplies are relatively abundant. Consequently, *M. sanguinipes* should benefit from rapid growth and energy accumulation, with concomitant high metabolic rates. A high Q_{10} and low nocturnal temperatures allow *M. sanguinipes* to conserve energy by reducing metabolic expenditures to very low levels at night.

In Deep Danyon, the activity season is long but food is scarce after the crop of spring annuals has disappeared, and high environmental temperatures preclude diurnal activity in much of the habitat. Hence, *T. pallidipennis* probably experience selection for an overall reduction in energy metabolism. The low Q_{10} in this species may be related to predator avoidance. Body temperatures of *T. pallidipennis* are about 20–25° C cooler at night than during the day. However, the animals are still alert and responsive at typical night-time T_b 's, and are capable of effective escape responses. This ability may be important, because nocturnally-active grasshopper predators are abundant and diverse in Deep Canyon (including rodents, snakes, lizards, toads, scorpions, and other arthropods). If the Q_{10} of *T. pallidipennis* was as high as that of *M. sanguinipes*, the nocturnal metabolic rate of *T. pallidipennis* would be 3.2 times lower than observed (assuming $\dot{V}O_2$ at the average diurnal T_b is the same). Such a reduction in metabolism might be reflected in a reduced ability to avoid predators. For example, *M. sanguinipes* cooled to typical nighttime T_b 's (also about 25° C below daytime values) are unresponsive and almost immobile. Predator pressure is probably considerably lower at Barcroft than in Deep Canyon, since the only potential nocturnal predators of *M. sanguinipes* are deer mice.

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