Metabolic Similarity Despite Striking Behavioral Divergence: Aerobic Performance in Low- and High-Density Forms of the Mormon Cricket

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ABSTRACT

Mormon crickets, large flightless katydids from western North America, occur in two forms that differ dramatically in population density and daily movement distances. The low-density form is small and cryptic and moves <1 m/d, while the high-density form is large and dark colored and travels up to 1–2 km/d in migratory bands. We determined daytime body temperatures and measured resting metabolic rate (RMR) and maximal aerobic metabolic rate (MMR) in forced exercise across a 10°–40°C temperature range. Field body temperatures were 15°–20°C in the morning and 25°–35°C during most of the day, and they never exceeded 40.6°C in either form. Mass-adjusted RMR and MMR were positively correlated across temperatures (significantly in some comparisons), indicating repeatability. Similarly, RMR was always positively and sometimes significantly correlated with MMR, suggesting a functional linkage between minimal and maximal aerobic performance. Factorial aerobic scopes (MMR/RMR) were highest at 10°C and declined at higher temperatures, but absolute scope (MMR − RMR) was highest between 30° and 40°C. Given the ca. 1,000-fold contrast in daily movement distances, we expected higher MMR and aerobic scope in the migratory high-density form. However, there were no differences between forms in RMR, MMR, aerobic scope, or ventilation patterns. The forms were also similar in metabolic response to temperature (Q_{10}) and in the mass scaling of metabolic rate. The absence of metabolic divergence among low- and high-density forms shows that large differences in locomotor behavior may not require concomitant changes in aerobic physiology.

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Introduction

A common assumption in ecological physiology is that behavior is functionally linked to suborganismal traits such as morphology, neuromuscular systems, and energy metabolism (Arnold 1983; Weibel 1984). Therefore, we expect variation in locomotor behavior among individuals, populations, or species to be correlated with differences in underlying physiological mechanisms. A well-studied example is aerobic capacity in mammals, which tends to be higher in "athletic" species than in more sedentary species (e.g., dogs vs. goats and ponies vs. calves [Taylor et al. 1981] and horses vs. steers [Jones et al. 1989]). Intraspecifically, groups with high locomotor activity often have greater aerobic capacity than less active groups; for example, aggressive and far-flying African honeybees (*Apis mellifera scutellata*) have higher flight metabolic rates than more docile and sedentary European honeybees (*Apis mellifera ligustica*; Harrison and Hall 1993). This effect can also be seen in responses to artificial selection on activity (e.g., genetic lines of mice selected for high voluntary running vs. control lines; Rezende et al. 2005) and to conditioning regimens such as exercise training, which often improve performance via changes in suborganismal traits, for example, cardiac and skeletal muscle mass (Kemi et al. 2002).

A striking example of highly divergent locomotor behavior occurs in the Mormon cricket *Anabrus simplex* Haldeman (Orthoptera: Tettigoniidae), a flightless shield-backed katydid native to western North America (Wakeland 1959). High-density populations of these large day-active insects are well known for their extraordinary migratory behavior. These populations undergo explosive outbreaks (Cowan 1929; MacVean 1987) and form dense bands (>50 crickets per m^2) that may contain millions of individuals. The bands undertake long-range migrations in search of high-protein foods and salt; they cannibalize each other and occasionally cause considerable damage to crops and rangeland (MacVean 1987; Gwynne 2001; Simpson et al. 2006). Migrating *A. simplex* typically move several hundred meters per day and sometimes up to 2 km/d (Cowan 1929; Lorch et al. 2005).

Low-density populations also occur, primarily in montane meadows on the eastern slope of the Rocky Mountains

(Gwynne 2001). These populations are solitary and sedentary. Mormon crickets from low-density populations typically move less than 1 m/d (Lorch et al. 2005), three orders of magnitude less than band-forming *A. simplex*.

The social and daily movement differences between high- and low-density populations affect population genetic structure (Bailey et al. 2007*b*). The forms also differ across many other traits. The low-density form has a cryptic greenish or brownish coloration, while the high-density form has a dark and possibly aposematic color. Individuals from high-density populations are larger, males sing with less vigor than low-density males (Bailey et al. 2007*a*), and the allometric relationship between the male forewing resonator and song carrier frequency differs between forms (Bailey et al. 2007*a*). Sex role reversal is common and consistent in high-density but not in low-density populations (Gwynne 1981, 1984).

Because of the interesting differences in morphology, behavior, and mating systems among forms and the economic importance of *A. simplex*, some additional aspects of their biology have been studied (e.g., feeding ecology; Redak et al. 1992; Simpson et al. 2006). However, we are aware of only one report of thermal relations and energetics of this species. Laffler et al. (2007) examined field body temperatures and metabolic rates but did not compare among forms or determine upper and lower limits of aerobic power output. Those issues are of interest because of the difference in daily movement distances and the correlation between aerobic capacity and exercise endurance in some species (e.g., Garland 1984; Garland and Bennett 1990; Koch and Britton 2005) and because the diurnal activity and open habitats of *A. simplex* may expose them to a range of thermal conditions. Here we describe body temperatures and gas exchange in Mormon crickets. We were particularly interested in temperatures attained in natural habitats, the thermal dependence of the upper and lower limits to aerobic energy metabolism, and whether the morphological and behavioral differences between forms are reflected in underlying physiological traits.

Material and Methods

Animals

Adults for physiological studies were collected during July of 2006 and 2007. We sampled high-density bands near Dinosaur, Colorado, in 2006 (40°30′13.7″N, 109°03′54.6″W) and Mountain City, Nevada, in 2007 (40°55′36.6″N, 115°53′02.1″W). Both locations experienced steady band activity over the previous decade. Low-density populations were sampled from two sites in the Poudre River canyon, about 65 km west of Fort Collins, Colorado: Kelly Flats in 2006 (40°40′41.8″N, 105°28′57.0″W) and Indian Meadows in 2007 (40°41′44.5″N, 105°31′35.2″W).

Animals were transported to our laboratory within 5 d of capture. We housed crickets in escape-proof cages in a secure room; fed them Purina rabbit chow, romaine lettuce, and apples; and maintained them between 20° and 25°C under a 14L : 10D cycle. Crickets maintained condition and were tested within 20 d of capture. All animals were killed at the conclusion of measurements.

Body Temperatures of Wild Crickets

To determine the thermal conditions experienced by wild Mormon crickets, we measured body and environmental temperatures in typical habitats. On 2 d in late June 1994, animals from several high-density bands in Dinosaur National Monument were sampled from roughly 0800 hours (local time) to dusk (about 2100 hours). In July 2007 we sampled low-density Mormon crickets from Indian Meadows in the Poudre canyon. All measurements were made on clear days with low winds.

Temperatures were recorded with a 24-gauge type-T thermocouple attached to an Omega HH23 thermometer. Before body temperature (T_b) measurement, individuals were observed, and their behavior was recorded (basking, walking, shade seeking), along with their location (on bare ground, litter, plants, etc.). We obtained T_b by grasping crickets and inserting the thermocouple through the abdomen into the center of the thorax within 1 s of capture. Stable thoracic temperature occurred within 3 s of insertion. Each individual was used for a single T_b measurement. Air temperature was measured in the space occupied by the sampled animal, and ground temperature was obtained by placing the thermocouple tip on the ground surface.

Metabolic Rate and Ventilation

We used open-circuit respirometry to measure CO_2 production ($\dot{V}CO_2$) and, for most individuals, oxygen consumption ($\dot{V}O_2$). Metabolism chambers were constructed from 30- or 60-mL plastic syringes by drilling a 6-mm-diameter hole near the rear of the barrel and gluing a plastic quick-connect fitting into the hole with silicon cement. Insects were sealed in the chamber with the syringe plunger, which seated against the tip of the quick-connect fitting, leaving an enclosed volume of about 20 mL (smaller syringes) or 50 mL. Air supplied by an upstream pump entered through the quick connect and exited through tubing attached to the other end of the syringe barrel. Flow rates (80–120 mL/min STP) were regulated with upstream mass flow controllers (Sierra Instruments, Monterey, CA, or Sensirion, Westlake Village, CA); water vapor and CO_2 were scrubbed from incurrent air (Dryerite and soda lime). Syringes were equipped with thermocouples for temperature monitoring (TC-1000; Sable Systems, Las Vegas).

Excurrent air was dried with magnesium perchlorate and flowed through a CO_2 sensor, either a Sable Systems CA-2A or a LiCor LI-6251 (LiCor Environmental, Lincoln, NE). Both resolved CO_2 to less than 5 ppm at low CO_2 concentrations (<1 ppm for the LI-6251). After exiting the CO_2 analyzers, air flowed through separate channels of a dual-channel O_2 analyzer (Sable Systems Oxilla; resolving about 5–10 ppm). Sensors were periodically referenced against dry CO_2-free air. The CO_2 sensors were calibrated weekly against a gas mixture containing 0.296% CO_2 in air. Drift between calibrations was negligible.

References and calibrations were done at the same flow rates and pressures used for measurements.

Outputs from gas analyzers and thermocouples were recorded every 1.0 s (maximum metabolism; resting metabolism in 2007) or 2.0 s (resting metabolism in 2006) on a Macintosh computer equipped with a Sable Systems UI-2 A-D converter and Warthog LabHelper software (http://www.warthog.ucr.edu). Metabolism chambers were housed in an environmental cabinet that maintained ambient temperature (T_a) ± 0.2°C. Timers controlled the light-dark cycle at 13L : 11D. Light intensities during the day were below 40 W/m^2 (much less than full sunlight, which is about 1,000 W/m^2).

Procedures for Measuring Metabolic Rates

For measurements of resting metabolic rate (RMR) and maximal metabolic rate (MMR), individual crickets were weighed (± 0.001 g) and sealed into a metabolism syringe. A plastic quick-connect piece was also placed in the syringe to give the animal something to grip. Temperature was adjusted to the desired value, and animals were left undisturbed for at least 30 min before measurements began. Immediately before measurements, a 2–5-min reference gas reading was obtained. We monitored gas exchange for at least 1 h at each T_a; occasionally, animals were left at one T_a for up to 12 h. Syringes were transparent, and we could observe activity. Also, active periods were obvious as episodes of high and irregular metabolic rate. Additional references were obtained at the conclusion of testing at a given T_a or every 1–2 h during long measurements.

We used Warthog LabAnalyst (http://www.warthog.ucr.edu) to adjust for gas baselines and calculate $\dot{V}CO_2$ and $\dot{V}O_2$. We assumed a constant respiratory quotient (RQ) of 0.85 and computed $\dot{V}CO_2$ as

$$\dot{V}CO_2 = \dot{V} \cdot \frac{F_eCO_2 - F_iCO_2}{1 - F_eCO_2 \cdot [1 - (1/RQ)]}, \quad (1)$$

where $\dot{V}$ is flow rate (STP), F_iCO_2 is the incurrent fraction of CO_2, and F_eCO_2 is the excurrent fraction of CO_2. Because CO_2 was scrubbed from incurrent air, F_iCO_2 was always 0. Use of a constant RQ may introduce calculation errors if the real RQ is different, but because F_eCO_2 was always quite small (<0.0024), the maximum introduced error was <0.3%. To improve response time we did not scrub CO_2 before O_2 analysis, and $\dot{V}O_2$ (mL/min) was calculated as

$$\dot{V}O_2 = \dot{V} \cdot \frac{(F_iO_2 - F_eO_2) - F_eO_2 \cdot (F_eCO_2 - F_iCO_2)}{1 - F_eO_2}, \quad (2)$$

where F_iO_2 and F_eO_2 are incurrent and excurrent O_2 fractional concentrations (F_iO_2 was 0.2095 and F_eO_2 was always >0.207), respectively. Because $\dot{V}O_2$ and $\dot{V}CO_2$ changed rapidly during MMR measurements, we used the instantaneous conversion (Bartholomew et al. 1981) to compensate for mixing and accurately resolve short-term changes. Effective volumes were 25–40 mL, depending on the size of the metabolic syringe.

When gas exchange was cyclic (Fig. 1*A*, 1*B*), we calculated RMR as the lowest continuous average that included an integral number of ventilation cycles (with a minimum of three cycles and a minimum duration of 10 min). When gas exchange was not cyclic (Fig. 1*C*), we used the lowest continuous 10-min average as RMR, excluding periods of activity. For tests where rest periods were frequently interrupted by activity, we used the lowest 5-min average. For animals with both $\dot{V}O_2$ and $\dot{V}CO_2$ data and noncyclic gas exchange, we searched for the lowest 5- or 10-min mean $\dot{V}O_2$ and determined $\dot{V}CO_2$ for the same interval.

At the conclusion of each RMR test, a reference reading was taken, and the respirometer was shaken vigorously (oscillatory movements about twice per second, plus tilting up and down at 40°–70° angles every few seconds) for 5 min. This, along with jostling from the quick-connect piece, elicited considerable locomotor activity. For most crickets, $\dot{V}CO_2$ (and $\dot{V}O_2$) quickly rose, stabilized for 1–3 min, and then began to decline before the 5-min measurement was complete (Fig. 2). Nearly all individuals ceased activity before or shortly after shaking stopped, with concomitant rapid declines in metabolism; in many cases, the righting response was absent for several minutes (tested by inverting the syringes so that animals were on their backs). We used the highest continuous 1-min running average of $\dot{V}CO_2$ and $\dot{V}O_2$ during exercise as MMR. Given the short duration of tests and occasional asynchrony in O_2 uptake and CO_2 release (e.g., Fig. 2), we searched for the highest 1 min of $\dot{V}CO_2$ and $\dot{V}O_2$ independently.

We attempted to measure RMR and MMR at 10°, 20°, 30°, 35°, and 40°C, and for some crickets we also obtained data at 15°, 22°–25°, or 32°–33°C. Temperatures were presented in random order, and no individuals were tested at all T_a's. For a few initial tests at 10° and 35°C, syringe temperatures changed by up to 2.4°C by the end of MMR measurements because of the handling of metabolic syringes. For these tests we used the mean T_a during MMR measurements. Subsequently, a change in procedures eliminated fluctuations $> \pm 0.4$°C during MMR tests.

Analysis of Cyclic Ventilation

When gas exchange was cyclic by visual inspection (Fig. 1*A*, 1*B*), we used the wave analysis, time integration, and selective integration procedures in LabAnalyst to obtain data on ventilation frequency, the height and duration of peaks of $\dot{V}O_2$ and $\dot{V}CO_2$, and the fraction of $\dot{V}O_2$ and $\dot{V}CO_2$ that occurred during peaks.

Statistical Analyses

Insect metabolism is a power function of body mass, and within the physiologically tolerable range, it is typically an exponential function of T_b (Bartholomew 1981). Accordingly, we used $\log_{10}$ values of mass and metabolism in analyses. Comparisons among categorical variables (e.g., sex, form) were performed with ANCOVA with mass and T_a as covariates, as appropriate. Repeated-measures procedures were used when data included

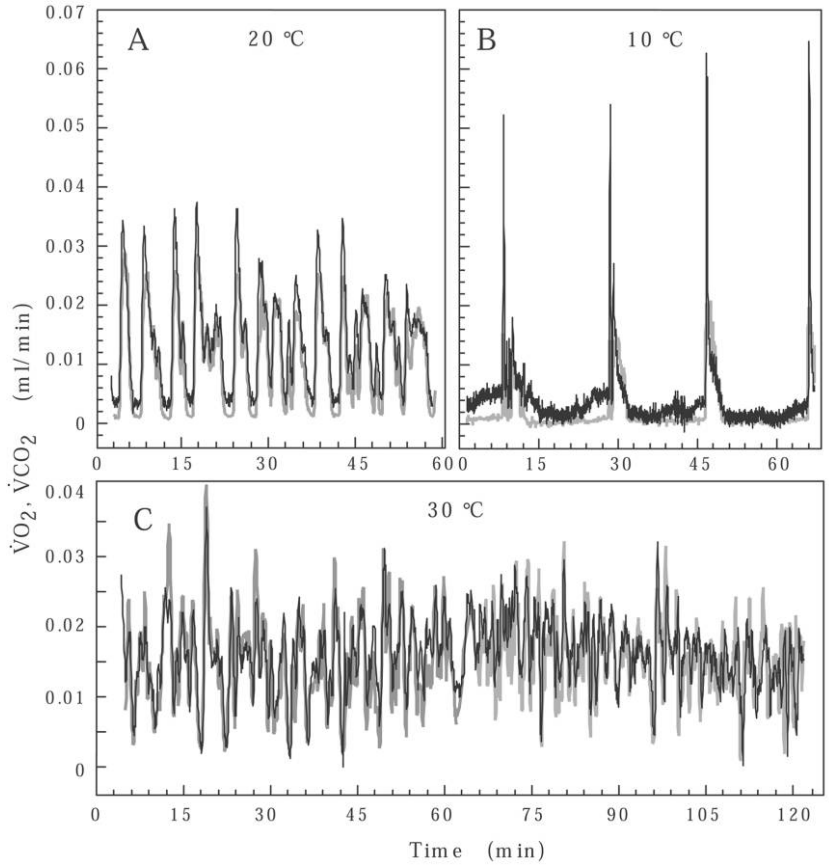

Figure 1. Examples of gas exchange in resting Mormon crickets *Anabrus simplex* at three ambient temperatures. Gray lines are rates of CO_2 production ($\dot{V}co_2$), and black lines are rates of O_2 consumption ($\dot{V}o_2$).

multiple measurements from individuals. Analyses were performed with SPSS, version 11, and SPSS, version 16 (SPSS, Chicago). Corrections for Type I errors in multiple simultaneous tests were done with sequential Bonferroni procedures (Rice 1989) or false discovery rates (FDRs; Benjamin and Hochberg 1995; Storey 2003). Results are expressed as means ± SD unless otherwise noted. The significance level (α) was 0.05 in most tests or 0.1 when we had an a priori directional expectation and used one-tailed tests.

Results

Body Temperatures in Wild Mormon Crickets

Relationships between body and air temperature and distributions of T_b during the day were similar in low- and high-density populations (Fig. 3). When air and ground temperatures were low, as was typical before 1000 hours (local time), both forms frequently sun basked. Migratory bands usually traveled from midmorning to midafternoon. Shade seeking and roosting in shrubs occurred when air and ground temperatures were high, particularly in midafternoon to late afternoon.

In both forms, daytime T_b was typically between 25° and 35°C, and the highest measured T_b was 40.6°C (Fig. 3*B*). Direct sunlight and ground temperatures substantially higher than 40°C were often available (Fig. 3*A*), so, presumably, crickets could have attained higher T_b. Mean T_b was slightly higher for low-density crickets (33.1° ± 3.5°C vs. 30.2° ± 5.5°C; $P < 0.001$). However, after adjusting for ground and air temperatures, T_b did not differ between forms (ANCOVA with air and ground temperature as covariates; $F_{1,200} = 2.29$, $P = 0.132$), with adjusted mean T_b of 30.6° ± 0.3°C (± SE) for high-density populations and 31.4° ± 0.4°C for low-density populations.

Animals for Metabolic Studies

We measured gas exchange in 61 Mormon crickets (Table 1). ANOVA revealed significant effects of sex ($F_{1,53} = 32.9$, $P < 0.0001$), form ($F_{1,53} = 168$, $P < 0.0001$), and year ($F_{1,53} = 22.9$, $P < 0.0001$) on body mass, with a significant form-by-year interaction ($F_{1,53} = 35.3$, $P < 0.0001$; other interaction terms were not significant). Animals from high-density populations, particularly males, were heavier in 2007 than in 2006, but low-density forms were heavier in 2006, and the proportional difference was smaller than for high-density forms. When data were pooled from both years, mean body mass for high-density forms was 4.70 ± 0.89 g (females) and 3.915 ± 0.995 g (males); for low-density forms, mean mass was 2.67 ± 0.43 g (females) and 1.93 ± 0.23 g (males).

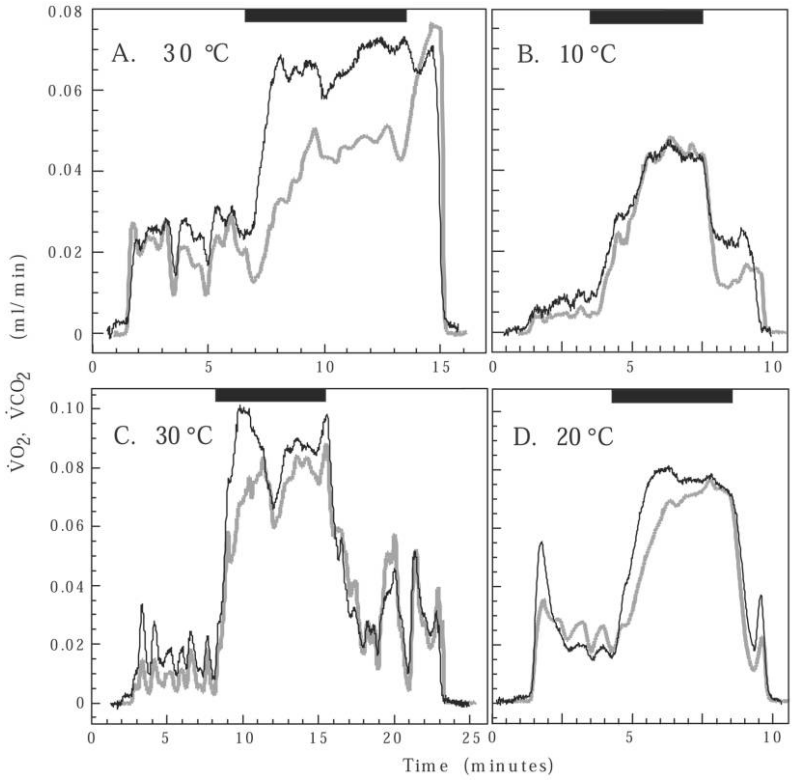

Figure 2. Examples of maximal rates of oxygen consumption ($\dot{V}o_2$; *black lines*) and carbon dioxide production ($\dot{V}co_2$; *gray lines*) during forced exercise in Mormon crickets *Anabrus simplex*. Black bars show periods of forced activity.

Resting and Maximal Metabolism across Temperatures

We measured metabolism at overlapping T_a in 2006 (10°, 15°, 20°, 25°, 30°, and 35°C) and 2007 (23°, 30°, 35°, and 40°C). There was some T_a variation among measurements, so when comparing among T_a's in ANOVA or ANCOVA, we pooled data within ± 1.0°C. To test for year effects, we compared data obtained in both years at 30° and 35°C, using ANCOVA with sex and form as fixed effects and body mass as covariate. Year had no effect on RMR or MMR ($\dot{V}o_2$ or $\dot{V}co_2$) at either T_a ($P > 0.20$ in all cases), so we excluded year from subsequent analyses.

We tested for effects of sex and form using repeated-measures ANCOVA at three or four temperatures in each year (10°, 20°, and 30°C in 2006; 23°, 30°, 35°, and 40°C in 2007), with mass as covariate (Table 2). For both resting and maximal $\dot{V}o_2$, there were no significant effects of sex ($P > 0.06$) or form ($P > 0.2$). Qualitatively identical results were obtained for resting and maximal $\dot{V}co_2$ (for both sex and form, $P > 0.3$ for MMR and RMR). No interaction terms were significant for either $\dot{V}o_2$ or $\dot{V}co_2$.

Because no individuals were measured at all T_a's, we also tested for effects of sex and form on MMR and RMR by pooling all animals within each T_a range, using simple ANCOVA with mass as covariate. Form was never a significant factor, and sex was significant only for $\dot{V}o_2$ MMR at 10°C (significance disappeared in an FDR test). Accordingly, sexes and forms were pooled for analyses of metabolic rate.

Metabolism was strongly influenced by mass and T_a. RMR increased steadily with increasing T_a between 10° and 40°C; MMR varied similarly between 10° and 30°C but plateaued between 30° and 40°C (Fig. 4). A multiple regression of $\log_{10}$RMR, $\log_{10}$mass, and T_a explained most variation in RMR: $\log_{10}\text{RMR (mL O}_2\text{/min)} = -2.85 + 0.566 \cdot \log_{10}\text{mass} + 0.0341 \cdot T_a$ ($F_{2,214} = 659$, $P < 0.0001$, $r^2 = 0.860$). Results were similar for $\dot{V}co_2$: $\log_{10}\text{RMR} = -3.027 + 0.452 \cdot \log_{10}\text{mass} + 0.0393 \cdot T_a$ ($F_{2,243} = 783$, $P < 0.0001$, $r^2 = 0.866$). Thus, resting $\dot{V}o_2$ from 10° to 40°C had a Q_{10} of 2.19 and varied as mass$^{0.566}$, while resting $\dot{V}co_2$ over the same T_a range had a Q_{10} of 2.47 and varied as mass$^{0.452}$. For both $\dot{V}o_2$ and $\dot{V}co_2$, there were no differences between low- and high-density forms in either Q_{10} or mass exponents ($P > 0.15$).

After we corrected for mass and T_a, considerable variance remained in RMR and MMR (Fig. 4). Variation in RMR could result from activity. To test this, we compared RMR with and without the presence of cyclic or discontinuous gas exchange (DGC), which in most insects is thought to occur only during inactivity (e.g., Chown et al. 2005). We never observed DGC in active *Anabrus simplex*. Because Mormon crickets rarely exhibited DGC at $T_a > 25$°C, we restricted our comparison to 10°–25°C. ANCOVA (mass and T_a as covariates) revealed no difference in RMR when DGC was present ($N = 38$) or absent

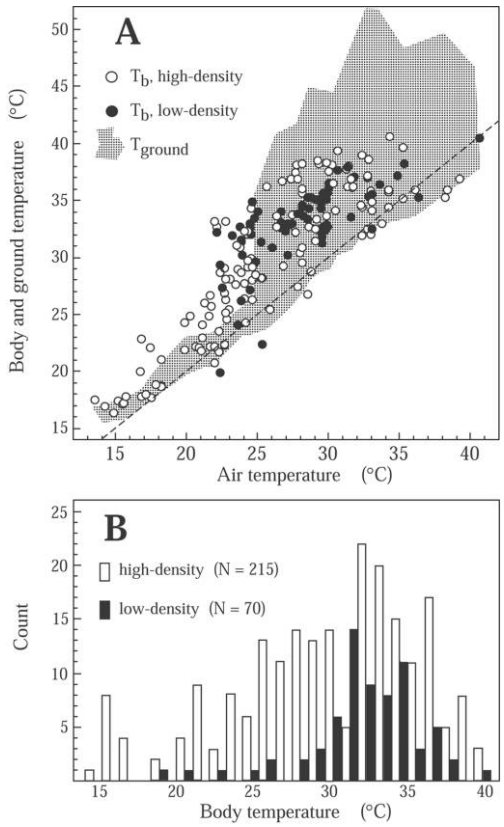

Figure 3. *A*, Body and ground temperature as a function of air temperature for Mormon crickets *Anabrus simplex*. *B*, Frequency distribution of field body temperatures in low- and high-density forms.

($N = 46$; $F_{1,80} = 0.003$, $P = 0.98$), indicating that activity was not responsible for residual RMR variation.

As for RMR, mass and T_a explained most of the variance in MMR. From 10° to 30°C, $\log_{10}$MMR (mL O_2/min) $= -1.969 + 0.575 \cdot \log_{10}\text{mass} + 0.0242 \cdot T_a$ ($F_{2,132} = 156$, $P < 0.0001$, $r^2 = 0.702$). For this T_a range, the Q_{10} for MMR $\dot{V}O_2$ was lower (1.75) than that for RMR $\dot{V}O_2$ (ANCOVA for categorical T_a from 10°–30°C; metabolic state-by-T_a interaction: $F_{4,229} = 15.5$, $P < 0.0001$). Results for $\dot{V}CO_2$ were similar: $\log_{10}\text{MMR} = -1.910 + 0.521 \cdot \log_{10}\text{mass} + 0.0224 \cdot T_a$ ($F_{2,143} = 142$, $P < 0.0001$, $r^2 = 0.664$); thus, Q_{10} was 1.675, and $\dot{V}CO_2$ varied as mass$^{0.521}$. The Q_{10} for $\dot{V}CO_2$ RMR and MMR differed significantly (ANCOVA for T_a from 10°–30°C; metabolic state-by-T_a interaction: $F_{4,264} = 24.4$, $P < 0.0001$).

Maximal metabolism plateaued at T_a above 30°C (Fig. 4). Temperature did affect MMR between 30° and 40°C, but Q_{10} was much less than for 10°–30°C. For $\dot{V}O_2$, the Q_{10} from 30° to 40°C was 1.31, and for $\dot{V}CO_2$, it was 1.29: $\log_{10}\dot{V}O_2$ MMR $= -1.64 + 0.588 \cdot \log_{10}\text{mass} + 0.01215 \cdot T_a$ ($F_{2,125} = 75$, $P < 0.0001$, $r^2 = 0.544$), $\log_{10}\dot{V}CO_2$ MMR $= -1.60 + 0.536 \cdot \log_{10}\text{mass} + 0.01111 \cdot T_a$ ($F_{2,129} = 79$, $P < 0.0001$, $r^2 = 0.488$). If the plateau at high T_a is ignored, the overall scaling for MMR from 10° to 40°C is to mass$^{0.620}$ (SE ±0.049; $r^2 = 0.729$) for $\dot{V}O_2$ and to mass$^{0.557}$ (SE ±0.049; $r^2 = 0.700$) for $\dot{V}CO_2$.

Because of different Q_{10} for RMR and MMR and the low Q_{10} for MMR at high T_a, factorial aerobic scope (MMR/RMR) was greatest at low T_a (Fig. 4). Mean factorial scope for $\dot{V}O_2$ in a 3.5-g cricket was 7.6 at 10°C, declining to 2.5 at 40°C (Fig. 5*A*; ANCOVA with T_a as a discrete variable and mass as covariate: $F_{6,187} = 21$, $P < 0.0001$). Scope for $\dot{V}CO_2$ in a cricket of similar mass was 12.3 at 10°C, falling to 2.7 at 40°C ($F_{6,210} = 30$, $P < 0.0001$). Although the relationship between scope and T_a had an inflection point at about 30°C (Fig. 5), factorial scopes continued to decline as T_a rose from 30° to 40°C (for $\dot{V}O_2$, $F_{2,119} = 5.7$, $P = 0.0011$; for $\dot{V}CO_2$, $F_{2,128} = 6.8$, $P = 0.00026$).

In contrast to factorial scope, absolute scope (MMR − RMR), which presumably indicates the aerobic power available to support activity, increased with increasing T_a for both $\dot{V}O_2$ (Fig. 5*B*; ANCOVA with T_a as a discrete variable and mass as covariate: $F_{6,185} = 22.5$, $P < 0.0001$) and $\dot{V}CO_2$ ($F_{7,208} = 18.5$, $P < 0.0001$). Absolute scope for $\dot{V}O_2$ increased 3.5-fold from 0.0264 mL/min at 10°C to 0.0915 mL/min at 40°C (adjusted to the mean mass of 3.51 g). Absolute scope for $\dot{V}CO_2$ increased 3.0-fold over the same T_a range, from 0.0301 to 0.0907 mL/min (adjusted to the mean mass of 3.41 g).

Unlike factorial scope, absolute $\dot{V}O_2$ scope was unaffected by T_a between 30° and 40°C ($F_{2,118} = 2.2$, $P = 0.11$), with a mass-adjusted mean of 0.0863 mL/min for a 3.61-g animal. Results over the same T_a range were similar for $\dot{V}CO_2$ ($F_{2,126} = 0.72$, $P = 0.54$), with a mass-adjusted mean of 0.0848 mL/min for a 3.54-g animal.

Respiratory Quotients

Repeated-measures ANCOVA (mass as covariate) for 2007 data (23°, 30°, 35°, 40°C) found no effect of mass, sex, form, or T_a on RQ ($\dot{V}CO_2/\dot{V}O_2$) in either RMR or MMR ($P > 0.16$). Similarly, in 2006 (10°, 20°, 30°C) there was no influence of these parameters on RQ during RMR ($P > 0.3$). For MMR, sample sizes

Table 1: Body mass (mean ± SD) in Mormon crickets by sex, form (low or high density), and year

Sex, Form, Year	Mass (g)	*N*
Female:		
High density:		
2006	3.900 ± .375	5
2007	5.035 ± .748	12
Low density:		
2006	2.880 ± .226	3
2007	2.595 ± .475	8
Male:		
High density:		
2006	2.829 ± .369	7
2007	4.607 ± .500	11
Low density:		
2006	1.945 ± .295	6
2007	1.915 ± .196	9

Table 2: Repeated-measures ANCOVAs of the effects of sex and form (high density vs. low density) on resting metabolic rate (RMR) and maximal metabolic rate (MMR)

Year, Trait	*N*	*F* Sex	*P* Sex	*F* Form	*P* Form	*F* Sex × Form	*P* Sex × Form
2006:							
MMR $\dot{V}O_2$	5 F, 9 M, 5 H, 9 L	4.23	.064	1.53	.24	.12	.74
MMR $\dot{V}CO_2$	5 F, 11 M, 7 H, 9 L	1.03	.33	.66	.43	.10	.76
RMR $\dot{V}O_2$	5 F, 8 M, 7 H, 6 L	.003	.96	.025	.88	.21	.66
RMR $\dot{V}CO_2$	7 F, 12 M, 10 H, 9 L	.325	.58	.10	.76	1.31	.27
2007:							
MMR $\dot{V}O_2$	8 F, 9 M, 10 H, 7 L	.007	.94	.06	.81	.05	.82
MMR $\dot{V}CO_2$	8 F, 9 M, 10 H, 7 L	.003	.96	.19	.67	.41	.53
RMR $\dot{V}O_2$	8 F, 11 M, 11 H, 8 L	.10	.75	.11	.74	.28	.61
RMR $\dot{V}CO_2$	8 F, 11 M, 11 H, 8 L	1.0	.33	.04	.84	.72	.41

Note. Temperature range was a categorical variable, and body mass was included as a covariate; $\log_{10}$ values of metabolic rate and body mass were used in analyses. Separate sets of individuals were used in 2006 (tested at 10°, 20°, and 30°C) and 2007 (tested at 23°, 30°, 35°, and 40°C). $\dot{V}O_2$ = rate of O_2 consumption; $\dot{V}CO_2$ = rate of CO_2 production; M = male; F = female; L = low-density form; H = high-density form.

were small in 2006 ($N = 2$ for some combinations of sex, form, and T_a), but RQ was affected by T_a ($F_{1,9} = 6.45$, $P = 0.032$), mass ($F_{1,9} = 5.85$, $P = 0.039$), sex ($F_{1,9} = 7.18$, $P = 0.025$), and form ($F_{1,9} = 5.70$, $P = 0.041$). There was no sex-by-form interaction ($P = 0.58$).

Because few data were available for repeated-measures analysis at multiple T_a's and no individuals were measured at all T_a's, we also tested for effects of mass, sex, form, and T_a using simple ANCOVA. In RMR, RQ was affected by mass ($F_{1,213} = 9.72$, $P = 0.0021$) and T_a ($F_{1,213} = 32.0$, $P < 0.0001$), but sex and form were not significant ($P > 0.12$), and there were no significant interactions. From multiple regression ($RQ = 0.761 + 0.0069 \cdot T_a - 0.0315 \cdot \text{mass}$; $F_{2,216} = 19.8$, $r^2 = 0.155$), the predicted RQ for a resting 2-g cricket increased from 0.755 at 10°C to 0.974 at 40°C; for a 5-g animal the corresponding change was 0.673 to 0.880. Similarly, RQ during MMR tests was affected by mass ($F_{1,202} = 6.7$, $P = 0.0101$) and T_a ($F_{1,202} = 10.4$, $P = 0.00144$) but not by sex or form ($F_{1,202} < 2.1$, $P > 0.3$). From multiple regression ($RQ = 1.185 - 0.00432 \cdot T_a - 0.0205 \cdot \text{mass}$; $F_{2,207} = 12.4$, $r^2 = 0.107$), the predicted RQ for a 2-g cricket decreased from 1.101 at 10°C to 0.971 at 40°C; the corresponding values for a 5-g animal were 1.04 at 10°C and 0.910 at 40°C.

Repeatability of Metabolism

Repeatability of RMR and MMR across T_a was assessed from mass residuals within three T_a ranges in 2006 (10°–20°, 20°–30°, and 10°–30°C) and 2007 (23°–35°, 30°–40°, and 23°–40°C), for which >10 crickets were measured. Significant positive regressions of residuals from measurements at two T_a's show repeatability (Hayes and Chappell 1990). All such regressions in *A. simplex* had positive slopes (Table 3). Comparisons across T_a ranges of 10°–12°C were often significant (one-tailed tests) for RMR (both $\dot{V}O_2$ and $\dot{V}CO_2$), but repeatability was usually absent across wider T_a differences. MMR showed a similar pattern but had less repeatability than RMR. Repeatability tended to be higher for $\dot{V}CO_2$ than for $\dot{V}O_2$, but the pattern was not consistent.

To compare performance in RMR and MMR (i.e., whether an individual's RMR predicts its MMR), we used mass residuals generated within six T_a's for which >10 individuals were mea-

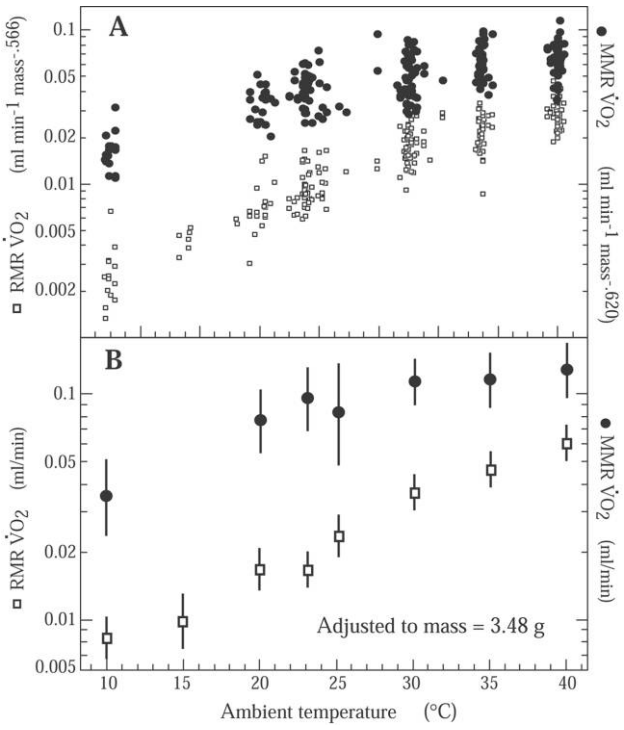

Figure 4. Metabolic rates (oxygen consumption, $\dot{V}O_2$) as a function of temperature in Mormon crickets *Anabrus simplex*. Data are pooled from both sexes and forms (low and high density). *A*, Mass-specific resting metabolic rate (RMR) and maximum metabolic rate (MMR; note slightly different mass scaling for RMR and MMR). *B*, Mean ± SE of RMR and MMR adjusted to a common body mass of 3.48 g (points shown only for temperature ranges containing three or more measurements).

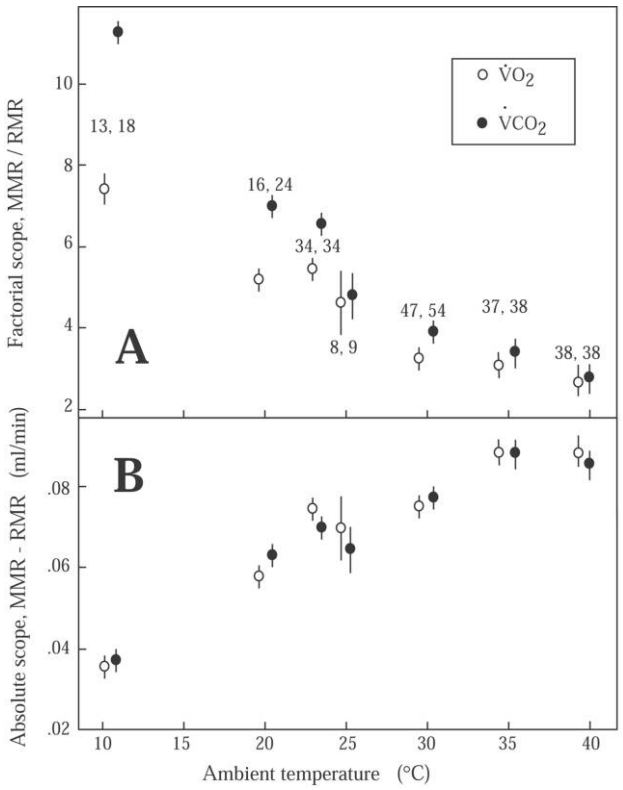

Figure 5. Effect of temperature on factorial scope (maximum metabolic rate [MMR]/resting metabolic rate [RMR]) and absolute scope (MMR − RMR) in Mormon crickets *Anabrus simplex*. Data are shown as mean ± SE at an adjusted mass of 3.5 g (oxygen consumption [$\dot{V}O_2$]) or 3.4 g (carbon dioxide production [$\dot{V}CO_2$]). For each temperature, numbers show N for $\dot{V}O_2$, followed by N for $\dot{V}CO_2$ (values are shown for temperature ranges containing three or more data points).

sured (10°, 20°, 23°, 30°, 35°, and 40°C; all $T_a \pm 1$°C). Correlations were always positive, but significance occurred only at high T_a (Table 4).

We also generated RMR and MMR residuals from multiple regressions with $\log_{10}$ body mass and T_a as predictors. This data set included all measurements from 10° to 30°C where crickets were tested for both RMR and MMR; data from higher T_a's were excluded because MMR plateaued above 30°C (Fig. 4). The data contained up to four measurements at different T_a's per individual. Correlations were positive and significant for both $\dot{V}O_2$ ($F_{1,115} = 10$, $P = 0.002$, $r = 0.283$) and $\dot{V}CO_2$ ($F_{1,135} = 7.2$, $P = 0.008$, $r = 0.226$). The analogous comparison for 30°–40°C data yielded similar results (for $\dot{V}O_2$, $F_{1,120} = 15.2$, $P < 0.0001$, $r = 0.335$; for $\dot{V}CO_2$, $F_{1,129} = 12.5$, $P = 0.00056$, $r = 0.297$).

Gas Exchange Cycles

The occurrence of discontinuous ventilation (where $\dot{V}O_2$ and $\dot{V}CO_2$ periodically fell to 0, presumably because spiracles were shut; Fig. 1*B*; Lighton 1998; Chown et al. 2005) or cyclic ventilation (where gas exchange oscillated rhythmically and reached low but nonzero rates; Fig. 1*A*) was unaffected by sex or form (ANCOVA with T_a as covariate $P > 0.5$). It occurred only in inactive crickets and was strongly influenced by T_a. Most individuals displayed cyclic gas exchange at low T_a, but its incidence declined rapidly as T_a increased (Fig. 6; $F_{1,6} = 34.6$, $P = 0.00107$, $r^2 = 0.852$). Quiescent crickets at high T_a usually exhibited irregular gas exchange patterns (e.g., Fig. 1*C*).

Usually, O_2 uptake was closely synchronized with CO_2 release, although in true discontinuous ventilation at 10°–20°C, O_2 uptake often rose slightly a few minutes before large bursts of O_2 uptake and CO_2 release; this is consistent with a flutter phase (Fig. 1*B*; Chown et al. 2005). At higher T_a, $\dot{V}O_2$ and $\dot{V}CO_2$ occurred in close synchrony, and both reached low but nonzero levels between bursts (Fig. 1*A*).

Repeated-measures ANCOVA (mass as covariate) at 10°, 20°, and 30°C or simple ANCOVA across all T_a's (mass as covariate) revealed no effects of sex or form on any ventilation parameter (frequency, peak heights for $\dot{V}O_2$ or $\dot{V}CO_2$, percent of gas exchange in peaks vs. interpeak periods, percent of cycle time in peaks vs. interpeak periods; $P > 0.08$ in all cases). Accordingly, sexes and forms were pooled for subsequent analyses. Multiple regression revealed no effect of mass on ventilation (Table 5), but T_a influenced several parameters, especially frequency, which increased approximately linearly with T_a (frequency = $-0.132 + 0.0196 \cdot T_a$; $F_{1,58} = 29.6$, $P < 0.0001$, $r^2 = 0.338$). Frequency averaged 0.064/min at 10°C (period = 15.6 min), rising 10-fold to 0.652/min at 40°C (period = 1.53 min).

Discussion

Our primary goal was to determine whether high- and low-density populations of Mormon crickets differ in aerobic physiology, in light of their striking divergence in daily movements. Interpreting such comparisons is aided by knowledge of the forms' phylogenetic status, so we begin with a brief review of distributions and population genetics in *Anabrus simplex*.

Genetic Relationships among Forms

High- and low-density forms are closely related (they readily interbreed; N. W. Bailey, unpublished data), but in addition to patterns of movement and dispersal, they differ in geographic distribution, size, color, and calling and mating behavior. The forms broadly correspond to a longitudinal mitochondrial DNA division, with low-density populations predominant in the eastern part of the range and high-density populations predominant in the west. The genetic division is best explained by Pleistocene vicariance: mtDNA and microsatellite evidence indicates that Mormon crickets were subdivided into separate refugia on either side of the Rocky Mountains during repeated glacial cycles (Bailey et al. 2007*b*). However, short-term behavioral flexibility occurs independently of the forms' separate evolutionary histories (Bailey et al. 2007*b*). For example, large, darkly pigmented but behaviorally solitary and sedentary crickets from the western mtDNA clade are common in areas where high-density bands underwent migrations in previous years

Table 3: Repeatability of Mormon cricket resting metabolic rate (RMR) and maximum metabolic rate (MMR) across temperatures for oxygen consumption ($\dot{V}O_2$) and CO_2 production ($\dot{V}CO_2$)

Temperature (°C), Gas	RMR			MMR		
	F (df)	*r*	*P*	*F* (df)	*r*	*P*
10–20:						
$\dot{V}O_2$	11.7 (1, 12)	.702	**.0051**	4.91 (1, 13)	.524	.045
$\dot{V}CO_2$	10.2 (1, 19)	.588	**.0051**	13.0 (1, 16)	.670	**.0023**
20–30:						
$\dot{V}O_2$	6.13 (1, 12)	.581	**.029**	.13 (1, 16)	.09	.72
$\dot{V}CO_2$	14.5 (1, 19)	.658	**.0012**	.14 (1, 19)	.085	.71
10–30:						
$\dot{V}O_2$	4.34 (1, 12)	.515	**.059**	.70 (1, 14)	.219	.42
$\dot{V}CO_2$	10.1 (1, 19)	.590	**.0049**	2.57 (1, 17)	.362	.127
23–35:						
$\dot{V}O_2$	.31 (1, 29)	.103	.58	.44 (1, 27)	.127	.51
$\dot{V}CO_2$	8.08 (1, 29)	.467	**.0081**	1.27 (1, 27)	.212	.27
30–40:						
$\dot{V}O_2$	3.42 (1, 28)	.330	**.075**	18.2 (1, 28)	.628	**.00020**
$\dot{V}CO_2$	2.90 (1, 28)	.306	.100	29 (1, 28)	.713	**<.0001**
23–40:						
$\dot{V}O_2$	5.03 (1, 29)	.384	**.033**	1.4 (1, 26)	.228	.24
$\dot{V}CO_2$	1.98 (1, 29)	.253	.17	14.2 (1, 26)	.595	**.00085**

Note. The 10°–20°, 20°–30°, and 10°–30°C repeatabilities were obtained in 2006, and the 23°–35°, 30°–40°, and 23°–40°C repeatabilities were obtained in 2007. *P* values in boldface indicate significance (one tailed) following pFDR tests (Storey 2003). For RMR, *P* values <0.0125 remain significant following sequential Bonferroni test (Rice 1989). For MMR, *P* values <0.011 remain significant after a sequential Bonferroni test.

(Bailey et al. 2008). That suggests that the behavioral phenotypes could be manifestations of plasticity in response to environmental variation (phase polyphenism), as reported for other orthoperans (Kennedy 1956; Uvarov 1966; Applebaum and Heifetz 1999; Simpson et al. 2001).

Aerobic Performance Comparisons

Probably our most interesting finding is a lack of differences between forms in the limits to aerobic energy metabolism, despite an enormous contrast in daily movement distances (Lorch et al. 2005). We also found similar daytime body temperatures and ventilation patterns. These results are noteworthy regardless of whether the forms are products of genetic divergence or phase polyphenism: in either case an obvious conclusion is that at least in some taxa, very extensive changes in behavior—even an energetically costly behavior such as locomotion—can be accomplished without adjusting the limits to aerobic power production.

Two caveats must be considered. First, it is conceivable that we did not accurately determine resting or maximal metabolism. We are confident that the RMR data are satisfactory because we used standard methods: temperatures were stable, animals were inactive, and we computed RMR only from periods when gas exchange was low and constant. The MMR data warrant closer scrutiny. Our protocol was designed to exercise crickets at intensities above those sustainable by aerobic respiration; this was expected to elicit maximal aerobic power production and rapid exhaustion. Crickets appeared exhausted at the end of measurements: most stopped struggling immediately after chamber oscillation ceased, and when inverted, many did not right themselves. It is possible that the cessation of moment and absence of righting response were due to disorientation instead of exhaustion, however. We did not measure lactate levels (an indicator of anaerobic ATP production), but RQ at MMR was usually higher than during RMR, consistent with use of anaerobic pathways (Harrison et al. 1991; Kirkton et al. 2005). Also, aerobic scopes of Mormon crickets are similar to those of other pedestrian ectothermic insects (e.g., Herreid et al. 1981; Herreid and Full 1984; Bartholomew et al. 1985; Full 1997; Rogowitz and Chappell 2000). Therefore, we assume that our MMR data are an accurate index of maximal aerobic power output in intensely exercised *A. simplex*, although we cannot be certain that higher metabolism could not be achieved in some other activity.

Probably a more relevant caveat is that MMR may not limit routine walking. Migrating Mormon crickets appear to travel at a moderate pace; we speculate that most walking is at submaximal power levels and does not generate exercise conditioning or selection for increased MMR. In a comparison worth noting, despite vast phylogenetic distance, the few mammals for which voluntary exercise costs are known rarely use speeds

Table 4: Correlations between resting metabolic rate and maximum metabolic rate in Mormon crickets

Temperature (°C), Gas	*N*	*R*	*P*
10:			
O_2	12	.232	.466
CO_2	18	.048	.851
20:			
O_2	14	.115	.682
CO_2	22	.116	.599
23:			
O_2	33	.210	.234
CO_2	33	.047	.790
30:			
O_2	46	.260	.0778
CO_2	53	.352	**.0090**
35:			
O_2	34	.300	.080
CO_2	34	.128	.464
40:			
O_2	37	.643	**<.0001**
CO_2	37	.507	**.00115**

Note. Correlations are based on residuals from regressions of $\log_{10}$ metabolic rate against $\log_{10}$ body mass. Data from 10°, 15°, and 20°C were obtained in 2006, and data from 23°, 35°, and 40°C were obtained in 2007; data from 30°C were obtained in both years. Temperatures are ±0.5°C. *P* values in boldface indicate significance (one tailed) following a pFDR test (Storey 2003) or sequential Bonferroni correction (for the latter, *P* values <0.0099 remain significant).

close to maximum aerobic speed (Chappell et al. 2004, 2007; but see Kenagy and Hoyt 1989). Instead of MMR, other locomotor traits might have diverged in *A. simplex*. For example, we did not test endurance at submaximal exercise, and the mobile high-density form may have increased endurance. Some evidence, although not consistent among studies, suggests that endurance is positively correlated with maximal aerobic capacity in a variety of species (e.g., lizards and snakes [Garland 1984; Garland and Else 1988; Garland and Bennett 1990], rats [Koch and Britton 2005], and human athletes [Craig et al. 1993]). Similarly, we did not measure energy costs of transport, which might be lower in the high-density form. That would permit less costly and hence faster and more extensive movement despite no difference in MMR (e.g., Full and Tullis 1990). We consider that scenario unlikely. Among mammals, costs of running are closely scaled to body mass (Taylor et al. 1981), and evolutionary modifications for greater running ability usually involve increased aerobic capacity (Taylor et al. 1981; Jones et al. 1989; Lindstedt et al. 1991; Weibel and Hoppeler 2005). Also, "athletic" mammals often show morphological as well as physiological modifications (e.g., loss of digits and long, slender limbs in highly cursorial species), but the two forms of Mormon crickets show few morphological differences other than size and color.

Limits to Energy Metabolism

Given that the high- and low-density forms of *A. simplex* do not differ in RMR or MMR, how do they compare to other insects? A recent comprehensive study (Chown et al. 2007) predicted an RMR of 3.6 mW for a 3.0-g insect at 25°C. Our estimated RMR for a 3.0-g Mormon cricket at 25°C is slightly higher: 6.4 mW, assuming 20.5 J/mL O_2. In the only published study of metabolism in *A. simplex*, estimated $\dot{V}CO_2$ was 11.3 mW in the same conditions (Laffler et al. 2007; eq. [2], RQ assumed to be 1.0). However, it is unclear whether this is a valid RMR because animals were not observed during measurements and activity could have occurred.

An interesting aspect of metabolism in Mormon crickets is a low mass exponent: for RMR of both forms combined, $\dot{V}O_2$ scaled to mass$^{0.566}$ after adjusting for T_a, and the corresponding scaling for $\dot{V}CO_2$ was to mass$^{0.452}$. Within forms, mass exponents for RMR were also low, ranging from 0.281 (low density, $\dot{V}CO_2$) to 0.587 (low density, $\dot{V}O_2$). Theories of metabolic scaling are contentious (e.g., West et al. 1997; Kozlowski and Konarzewski 2004). Empirical support for the historical standard of scaling to mass$^{0.75}$ is controversial, but most analyses find mass exponents of 0.7–0.8 across broad taxonomic scales and 0.67–1.0 at lower levels (Chown et al. 2007). These are substantially higher than our results for *A. simplex*. Our data covered a small mass range (approximately fourfold, including both forms; roughly twofold within forms), and variance was substantial (Fig. 4). Nevertheless, 95% confidence intervals for RMR mass exponents ($\dot{V}CO_2$, 0.345–0.559; $\dot{V}O_2$, 0.468–0.664; both forms combined) did not include 0.75, although the upper confidence limit for $\dot{V}O_2$ approached 0.67.

Compared to the rich database for RMR, fewer data are available on maximal metabolic rates during terrestrial exercise

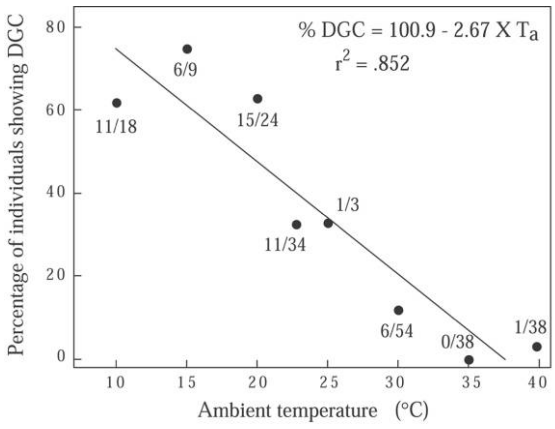

Figure 6. Temperature effects on the occurrence of discontinuous or cyclic gas exchange (DGC) in Mormon crickets *Anabrus simplex*. Data are pooled by temperature range (±1°C); numbers next to data points show numbers of individuals showing DGC versus the total number of individuals tested.

Table 5: Effects of temperature and $\log_{10}$ body mass on aspects of discontinuous gas exchange cycles (DGCs) in Mormon crickets

	Temperature			Mass			
Variable	*N*	*t*	*r*	*P*	*t*	*r*	*P*
DGC frequency	59	6.04	.624	**<.0001**	−2.28	−.289	.026
$\dot{V}CO_2$ peak duration as % of DGC	59	5.91	.616	**<.0001**	−1.17	−.154	.245
$\dot{V}CO_2$ peak amplitude	59	4.14	.481	**.00012**	1.38	.179	.174
% $\dot{V}CO_2$ in peaks	59	4.04	.472	**.00016**	−.474	−.063	.637
$\dot{V}O_2$ peak duration as % of DGC	38	3.35	.488	**.0019**	−.157	−.026	.876
$\dot{V}O_2$ peak amplitude	38	1.95	.308	.060	1.08	.177	.289
% $\dot{V}O_2$ in peaks	38	2.06	.324	.047	.705	.117	.486

Note. ANCOVA showed no effects of sex or form on the DGC. The table shows partial correlation coefficients and *P* values (two tailed) from multiple regression (temperature and $\log_{10}$ mass as predictors). *P* values in boldface indicate significance following a pFDR test (Storey 2003). For temperature, *P* values <0.0167 remain significant after a sequential Bonferroni adjustment. There were no significant effects of mass after either pFDR or Bonferroni tests.

in arthropods, and methods for eliciting and criteria for identifying MMR are not standardized. Many studies focused on energetics of locomotion and used treadmills to determine metabolism during sustained forced running (e.g., Herreid et al. 1981; Bartholomew et al. 1985); others employed voluntary running tubes (Lighton et al. 1993), motor-driven wheels (Rogowitz and Chappell 2000), or related devices. Few specifically tested for MMR. Comparisons are further complicated by endothermy in some species (e.g., Morgan 1987) and by large mass and phylogenetic differences. However, factorial aerobic scope (MMR/RMR) can provide useful insights across a wide size range. Factorial scope was ~3–10 in Mormon crickets, highest at low T_a (Fig. 5). Except at high T_a, those values are consistent with factorial scopes for other ectothermic insects: 3.4−12 in cockroaches (Herreid and Full 1984), about 10 for tenebrionid beetles (Bartholomew et al. 1985), 8 for ants (Lighton et al. 1987), 5.5–18 in cerambycid beetles (Rogowitz and Chappell 2000), 16 in rhinoceros beetles carrying weights (Kram 1996), and 6–25 in crickets, beetles, and cockroaches (Full et al. 1990). Because RMR is high in *A. simplex*, the species' relatively low scope at high T_a does not necessarily mean that its MMR is less than expected.

Similar to that in vertebrates (Weibel et al. 2004), the mass scaling for MMR in Mormon crickets tended to be higher than for RMR (slope differences were not significant, however). As for RMR, mass exponents for MMR were less than the ca. 3/4 scaling predicted by many theoretical analyses: 0.620 (±SE: 0.571–0.669) for $\dot{V}O_2$ and 0.557 (±SE: 0.508–0.606) for $\dot{V}CO_2$. The Q_{10} for MMR above 30°C was low, and MMR was fairly stable between 30° and 40°C (Fig. 4). To our knowledge, the plateau in *A. simplex* MMR at high but nonpathological T_a has not been reported in other insects.

At first glance, the low factorial scopes at the temperatures most frequently attained by Mormon crickets during the day (Figs. 3, 5*A*; Laffler et al. 2007) suggest reduced activity potential. However, absolute scope (MMR − RMR), the aerobic power assumed to be available to support activity, is highest between 30° and 40°C (Fig. 5*B*). Incremental costs of transport (the slope of the speed vs. metabolic rate relationship) are independent of temperature in ectothermic terrestrial vertebrates and insects (John-Alder and Bennett 1981; Lighton et al. 1993). Therefore, maximum aerobic running speeds are directly proportional to absolute scope, and it is likely that *A. simplex* can attain their highest sustainable speeds at 30°–40°C.

Repeatability across Temperatures and between RMR and MMR

The repeatability of performance traits is a key factor in how performance might be influenced by selection (Bennett 1987). There have been few measurements of metabolic repeatability in insects, but when tested these traits generally show significant repeatability (Chappell and Rogowitz 2000; Marais and Chown 2003; Nespolo et al. 2003). In our study we did not assess long-term trait consistency, but we did determine repeatability across T_a. Regressions of initial and final mass residuals of MMR and RMR always had positive slopes and were often significant (Table 3). Thus, individuals with high RMR at one T_a are likely to have high RMR at another T_a, and the same trend pertains to MMR.

The relationship between RMR and MMR is also of interest because it is often proposed that selection favoring high MMR (e.g., to support sustained activity) will also elevate RMR (e.g., Bennett and Ruben 1979). The postulated mechanism is increased maintenance costs for the larger or more active organs needed to support high MMR (e.g., increased power output in exercise requires more muscle as well as greater capacity in nutrient delivery and waste removal systems). Our results are consistent with this hypothesis, as we found positive and sometimes significant correlations between mass residuals of MMR and RMR (Table 4). In contrast, Rogowitz and Chappell (2000) reported no correlation between MMR and RMR in eucalyptus-boring beetles (*Phorocantha* sp.). The absence of consistency in RMR-MMR relationships in these insect species parallels the

situation among endothermic vertebrates, where correlations between minimal and maximal aerobic metabolism have been found in some species but not in others (Table 6 in Chappell et al. 2007).

Discontinuous and Cyclic Ventilation

The variable ventilation patterns in *A. simplex* (Table 5) are similar to cyclic and discontinuous ventilation in other insect taxa. Discontinuous ventilation is known to occur in eight insect orders (Chown et al. 2005), including orthopterans (Hadley and Quinlan 1993; Harrison et al. 1995; Rourke 2000), although it was not observed in a previous study of *A. simplex* (Laffler et al. 2007). Several adaptive explanations for DGCs have been proposed, but there is no consensus on the selective factors involved in their evolution or even whether they are adaptive (reviewed in Chown et al. 2005).

Our study was not designed to test concepts of DGC origins or adaptive value, but the results are relevant to one hypothesis of DGC evolution. The occurrence of cyclic or discontinuous ventilation in *A. simplex* declines with increasing T_a (Fig. 6). The prevalence of DGCs at low T_a and their almost complete absence at high T_a is inconsistent with the hygric hypothesis for DGC evolution: that DGCs are favored by selection as a means of restricting respiratory water loss (Chown et al. 2005). Because saturation vapor pressure in the trachea increases rapidly with rising body temperature, the hygric hypothesis predicts increasing use of DGCs at high temperatures: the opposite of what we found. A similar pattern was reported for eucalyptus-boring cerambycid beetles (Chappell and Rogowitz 2000); the authors speculated that these beetles may not experience strong selection for desiccation resistance because of water-rich diets. The same may be true for *A. simplex*, which feeds on moist plant material, supplemented with animal protein (Redak et al. 1992; Simpson et al. 2006).

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