The effects of mass and age on standard metabolic rate in house crickets

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Abstract. This study employed flow-through respirometry to measure the oxygen consumption rates ($V_{O_2}$) of inactive male house crickets, Acheta domesticus L. (Orthoptera: Gryllidae), and to quantify the effects of body mass and adult age on standard metabolic rate (SMR). The $V_{O_2}$ increased with male body mass at a rate similar to that found in other studies of insect aerobic metabolism. The data reported in this study are combined with published data from other species of Orthoptera to generate a consensus allometric relationship between SMR and body mass for the Order. In general, the Orthoptera expend 2–3 times the energy per unit of body mass when inactive as compared to other arthropods, such as tenebrionid beetles, ants and spiders. Possible explanations for this substantial difference are discussed. By contrast to body mass, mass-specific $V_{O_2}$ decreased with increasing male age. This age effect has previously been reported for mammals but is not well established for insects, and its implications for the preference of cricket females for older mates is discussed. As energy expended for metabolic maintenance comprises 78% of a male cricket’s daily energy budget, changes in SMR may have a substantial effect on the energy available for reproduction.

Key words. Standard metabolic rate, $V_{O_2}$, mass, age, Gryllidae, Orthoptera.

Introduction

Standard metabolic rate (SMR) is an important parameter to quantify for several reasons. First, it represents the energetic cost of simple subsistence for a poikilotherm, determining an individual’s minimum energy requirements under a standardized set of conditions. In this regard, it is a measure analogous to basal metabolic rate in homeotherms. In arthropods, this subsistence cost may constitute a significant fraction of total daily energy expenditure and thereby limit the resources available for reproduction (Zera & Rankin, 1989; Tanaka, 1993) or affect life-span (Lighton & Fielden, 1995).

Secondly, SMR increases with body size in animals (reviewed by Hemmingsen, 1960), but the scaling parameters of this allometric relationship vary among taxa (Heusner, 1985). Differences among taxonomic groups in this allometric relationship potentially reveal unique physiological adaptations (e.g. Lighton & Fielden, 1995) and provide an insight into the basis of this fundamental rule. It is unknown whether all insects share the same scaling parameters for the SMR-body size relationship since relatively few species and families have been investigated (review by Lighton & Fielden, 1995).

Thirdly, SMR is the basis for comparing the relative energetic costs of particular activities. Factorial scope, which expresses an activity’s metabolic cost as a multiple of SMR, allows comparisons of relative cost to be made across both species and broader taxonomic categories (e.g. Bartholomew et al., 1981; Burk, 1988). Accurate and consistent measurements of SMR are therefore critical to the utility of factorial scope as a measure of relative energetic expenditure and the validity of evolutionary explanations constructed from these comparisons. Ideally, measurements of SMR are made under constant environmental conditions on individuals of known mass, sex and age that show no external activity and are not actively digesting or noticeably stressed. However, because studies often differ in the conditions under which SMR is measured, it is particularly important to quantify the effect of specific environmental and phenotypic factors on SMR.

This study of SMR was undertaken as part of a larger investigation into the energetic costs of male fighting and mating behaviour in the cricket Acheta domesticus L. (Orthoptera, Gryllidae) (Hack, 1994, 1997b). Accurate measures of SMR are required to evaluate the relative fitness consequences of energy expenditures on alternative agonistic and mating
behaviours. Also, male body size varies substantially in this and other species of crickets (e.g. Simmons, 1988), with maximum body size in a population exceeding minimum body size by 2–3 fold. Large size confers an advantage in fighting success and possibly mating success (review by Simmons, 1995; Hack, 1997a). If males expend a large proportion of their daily energy budgets on simple metabolic maintenance, higher metabolic costs of subsistence for larger males, and therefore greater foraging demands, may possibly off-set the benefits of size and represent an important factor in shaping male life-histories and alternative mating strategies (Cade, 1979). Neither this proportion nor the scaling parameters for the body size-SMR relationship are adequately known for crickets.

An additional endogenous factor that possibly affects SMR in crickets is adult age. Mass-specific resting metabolic rates in adult humans and other mammals decrease with age (Fukagawa et al., 1990; McCarter & Palmer, 1992). Whether this relationship also occurs with the mass-specific SMR of adult insects is as yet unclear. Surprisingly few studies of insects have assayed mass-specific SMR among individuals of varying age. The rates of oxygen consumption by adult female Drosophila melanogaster and juvenile female A. domesticus decrease with age (Lints & Lints, 1968; Woodring et al., 1977), but the effect of age on mass-specific SMR is not clear in either example, as activity (e.g. feeding, locomotion, grooming) was not controlled. Reduced activity may account for the observed decreases in oxygen consumption, rather than an age-dependent effect on the amount of oxygen required for metabolic maintenance. Paradoxically, in the one known study focusing on age and inactive metabolic rate, mass-specific oxygen consumption at rest increased slightly over the first 20 days of adulthood for male desert locusts (Walker et al., 1970). Thus, further study is needed to establish whether SMR decreases with adult age in insects. This question is particularly relevant to the Gryllidae since evidence from several species indicates that females consistently prefer the sexual advertisement song of older males and prefer to pair with these males (Zuk, 1987, 1988; Simmons & Zuk, 1992; Simmons, 1995).

This study was designed primarily to measure the effects of body mass and adult age on the oxygen consumption rates of inactive adult male house crickets, and thus their aerobic SMR. However, several environmental factors are known to influence the aerobic metabolic rates of insects, including temperature, time of day and season (Keister & Buck, 1974; Woodring & Clifford, 1986). Accordingly, the effects of time of day (ambient light) and trial date on SMR were also considered, but temperature was controlled to minimize its influence. Flow-through respirometry was used to measure the oxygen consumption rates of individuals varying simultaneously in the several factors likely to affect SMR, and multiple regression was employed to distinguish statistically the independent influence of each. Comparable data for other Orthoptera were combined with those for A. domesticus to generate an allometric relationship between SMR and body mass for this insect Order.

Materials and Methods

The house crickets used in this study were derived from stocks bred for several generations in the laboratory. All study animals were descended from a single founding population (n = 500). The crickets were provided with food and water ad libitum and maintained at 23–26°C on a LD 12.5:11.5 h photocycle shifted forward so that full darkness began at 16:00 h.

Open-system (flow-through) respirometry was used to measure the oxygen consumption rates (VO2 as distinguished from volume of oxygen, V02) of crickets at complete rest. A dual-sensor respirometer (Applied Electrochemistry Inc. S–3A) continuously measured the oxygen concentration difference between a test chamber containing the experimental animal and an empty control chamber. Water and CO2 were removed from the chambers’ excurrent air streams prior to pulling them through the oxygen sensors at a controlled rate of 25 ml/min. The difference in excurrent O2 concentration between the two chambers, representing the amount of oxygen consumed by the test animal, was continuously calculated to a resolution of 0.001% (for further apparatus description refer to Hack, 1997b). A Macintosh computer running custom software polled the respirometer several times per second and averaged successive values to produce a single sample datum. Using the same software, continuous-time plots of differential O2 concentration were corrected for sensor drift, smoothed to remove noise, and corrected to reflect instantaneous rates of O2 consumption (Bartholomew et al., 1981) under dry, standard temperature and pressure (STPD) conditions. Because the use of instantaneous O2, or real-time measurements of aerobic metabolism, allowed very brief changes in oxygen consumption rates to be detected, periods of complete inactivity could be clearly distinguished from periods of sporadic activity. This ensured that measurements of SMR would only be estimated from periods of inactivity and thus be free of error introduced by brief grooming or other spurious movements (see below). As pointed out by Lighton & Wehner (1993), estimating SMR from non-instantaneous rates integrated over periods of several hours often results in large overestimates.

Stable experimental temperatures were maintained by placing both metabolic chambers and their associated plumbing on a water-tight Lucite platform immersed in a temperature-controlled water bath. The temperature within the control metabolic chamber was monitored continuously via a thermocouple and digital thermometer (Bailey Instruments BAT–12). Chamber air temperatures did not vary appreciably within any single trial (± 0.1°C) or within any set of trials per day (± 0.2°C). However, across the four days of trials, air temperature ranged from 24.7 to 26.6°C. To control for this variance, O2 was standardized for each trial to a temperature of 25°C, assuming a Q10 of 2.5 (Withers, 1992).

The respirometry chambers consisted of thick-walled (2.5 mm) plastic tubes 5 cm in length and capped with rubber bungs. Glass tubes inserted through the bungs created influx, efflux and thermocouple ports. The chamber’s small size restricted cricket movement yet resembled a natural resting place, such as a burrow or crevice. Its correspondingly small volume (8 ml) relative to the flow rate (25 ml/min) maximized
the detection of rapid changes in oxygen consumption and ensured adequate mixing for applying the instantaneous correction.

Test crickets were kept singly in containers and allowed to adjust to the experimental conditions for several hours before a trial began. No food was provided during this period in order to limit digestive activity, a possible source of error in measuring SMR. Single trials lasted 15 min. Only periods of complete inactivity were used in the measurement of SMR; each male was represented in the analysis by its single longest period of inactivity > 2 min. Inactivity was determined by continuous observation, from 40 cm away, of each male throughout the entire duration of a trial. In addition to conspicuous activities, such as walking, grooming and stridulation with the tegmina, single movements of the antennae, legs or abdomen were also noted, thus ensuring that measurements were only made during periods of complete external inactivity. Changes in \( \text{O}_2 \) caused by these movements, as during grooming, could usually be detected directly on the continuous oxygen consumption record, facilitating their exclusion from analysis. Other periods of brief activity were excluded from analysis after temporal alignment of the observation and oxygen consumption records.

A total of thirty-one trials were conducted between 1000–1800 hours, or from 6 h before, to 2 h after, darkness. Activity levels in this species are known to increase significantly over the progress from the light to dark phase of the daily cycle (Woodring & Clifford, 1986), but whether similar changes occur in SMR is not known. Experimental light levels were adjusted from full light (two 60 watt incandescent bulbs at 1.5 m), to half light (one 60 watt bulb at 1.5 m), to full darkness (red observation bulb only), corresponding to the crickets' normal daily light:dark cycle. Trials took place over the range of body size sampled in this study and decreased by 1\% over the range tested (b < 0.001, t = 0.37, P > 0.7), and consequently was excluded from the final regression model. Inspection of the partial regression of ln-transformed inactive \( \text{Vo}_2 \) on time of day confirmed the absence of any linear or simple curvilinear function relating these two variables.

Inspection of the partial regression functions reveals that expected inactive \( \text{Vo}_2 \) increased by 210\% over the natural range of body size sampled in this study and decreased by 19\% over a range in adult age from 7 to 81 days (Fig. 1). Over the nine week duration of the experiment, mean inactive \( \text{Vo}_2 \) per trial date differed by a maximum of 20\% (Fig. 2). The three variables of body mass, adult age and trial date together explained 81.7\% of the observed variance in mean inactive \( \text{Vo}_2 \). Body mass alone accounted for nearly 52\% of the observed variance in inactive \( \text{Vo}_2 \). The additions of age and trial date to the regression model increased the total explained variance in inactive \( \text{Vo}_2 \) by 22\% and 8\%, respectively. Intercorrelation among the explanatory variables was generally low (\( r < 0.4 \)) and not statistically significant for any variable pairs.

Assuming a translation factor of 20.1 J per ml \( \text{O}_2 \) (Elliot & Davison, 1975), inactive \( \text{Vo}_2 \) can be converted to aerobic SMR. The relationship between body mass and metabolic rate can then be expressed as:

\[
\text{SMR} = 2661 \cdot \text{mass}^{0.873} \text{ in } \mu\text{W at } 25^\circ\text{C}.
\]
The 95% confidence intervals for the slope and intercept parameters in this relationship are 0.600–1.146 and 2011–3518, respectively. Microwatts (μW), or units of energy metabolism per unit of time, have arbitrarily been chosen for the purposes of comparing metabolic rates across studies.

Similar transformation of published oxygen consumption rates while inactive for other orthopteran species (n = 11, Fig. 3) leads to a consensus interspecific relationship in this order of:

\[ \text{SMR} = 2710 \cdot \text{mass}^{0.961} \text{ in } \mu \text{W at } 25^\circ \text{C}. \]

The 95% confidence intervals for the slope and intercept parameters in this relationship are 0.680–1.242 and 1832–4010, respectively. The mean inactive VO2 of male house crickets quantified in this study falls well within the range of comparable measures produced for other Orthoptera (Fig. 3). The slope value obtained for Orthoptera resembles that determined by Lighton & Fielden (1995) as a consensus value for arthropods: 0.816, derived from data for 28 species of spiders, 11 species of beetles, and 16 species of ants. However,
the intercept of the orthopteran allometric relationship exceeds that of the arthropod consensus relationship (906) by nearly threefold.

**Discussion**

**Mass**

The increase in male house cricket SMR with body mass observed in this study was not an unexpected result. However, the rate of increase has a potentially important implication for male reproductive behaviour. SMR increased more than twofold over the natural body size range of A. domesticus males (Weissman et al., 1980). If the costs of subsistence constitute a large fraction of daily energy expenditure, a doubling of SMR should affect reproductive effort, either by decreasing the energy available for reproductive activity (e.g. calling to attract mates, spermatophore production) or by increasing foraging time (e.g. Zera & Rankin, 1989; Simmons, 1993; Tanaka, 1993). The estimated daily energy expenditure in A. domesticus can be calculated from known costs for the predominant activities of adult males (Hack, 1994, 1997b) and reasonable estimates of the frequency of each per day under natural conditions (i.e. 4000 steps or 40 m of travel, 10 fights, 6 h of advertisement calling and 10 min of courtship: French & Cade, 1989; Cade & Cade, 1992). (The daily energy budget estimated in this manner, 16.814 ml.g⁻¹.day⁻¹, is only 4% greater than the daily energy expenditure measured under semi-natural conditions in the laboratory: mean = 16.240 ml.g⁻¹.day⁻¹, n = 14, range = 9.350–22.326; Hack, 1997b). The mean SMR measured in this study, integrated over a 24-h period, then accounts for 78% of this estimated daily energy budget. Thus, the proportion of the daily energy budget allocated to metabolic maintenance is large for Grylline crickets and may play a more important role than has previously been recognized in shaping alternative male mating strategies (Cade, 1979; Cade & Cade, 1992). Large males may choose a more sedentary strategy of burrow defence in areas with abundant food, given their greater demand for nutrients, whereas smaller males can better afford to search widely for mates and exploit smaller patches of resources. Both mating strategies are present in several cricket species (review by Cade & Cade, 1992), but relatively little is known currently about male foraging behaviour and the influence of size-dependent metabolic demands on these strategies.

The interspecific scaling exponent relating body mass and SMR derived in this study for the Orthoptera agrees generally with that found for other groups of insects (Lighton & Fielden, 1995). Perhaps more important to the comparison of SMR across taxa is the mass-scaling coefficient of the allometric relationship (Heusner, 1985). In both the intraspecific relationship for A. domesticus and the interspecific relationship for Orthoptera, the scaling coefficient leads to SMR values two- to threefold those predicted by the consensus arthropod relationship derived by Lighton & Fielden (1995). This suggests that crickets, and Orthoptera in general, expend more energy at rest per unit mass than the arthropods surveyed by these researchers (see above). A greater proportion of body mass composed of metabolically active tissue may account for the greater SMR of Orthoptera. For example, relative to beetles, the orthopterans included in this study have reduced forewing mass (cf. tegmina to elytra) yet retain functional flight muscles for stridulation and/or flight. Also, they often have enlarged hind leg muscle mass relative to leg length. A unit mass of active metabolic tissue may also vary in its degree of activity (Sima, 1984), further contributing to variance in metabolic rate across taxa. Activities characteristic of orthopterans that may rely on highly active metabolic tissue include explosive jumping and acoustic signalling at high frequencies and amplitudes.

Alternative explanations for the relatively elevated metabolic rates of orthopterans include measurement error, stress from handling, and inadequate control of digestive activity. Many of the data used to determine the interspecific scaling coefficient were collected with closed-system respirometry over a period of several hours, a technique that controls poorly for spurious activity (Lighton & Wehner, 1993). However, the inherently more accurate estimates of SMR resulting from open-system, instantaneous measurement of V_{O₂} (e.g. Full et al., 1990; this study) did not differ substantially from those resulting from the closed-system data, as would be expected if the two techniques consistently produced highly divergent values. Inadequate control of stress or digestive activity probably added some error to the measurements of SMR obtained (see below). However, it seems unlikely that either of these extraneous factors would raise the SMR two- to threefold, given that vigorous activity such as stridulation raises the metabolic rate of A. domesticus by only 20–40% (Hack, 1997b).

In general, these factors probably contributed to the observed elevation of orthopteran SMR relative to those of other arthropod groups, but they do not appear to account entirely for the greater than twofold disparity. More measurements of SMR employing open-system respirometry are clearly needed to establish the generality of elevated metabolic rates in the Orthoptera.

**Time of day and trial date**

Male SMR in this study did not significantly change with time of day, or across the transition from the light to dark phase of the photocycle. Several cricket species, including A. domesticus, demonstrate daily rhythms in locomotion, feeding and reproductive behaviour (Cymborowski, 1973; Honegger, 1981; Woodring & Clifford, 1986; Loher, 1989). Oxygen consumption rhythms in adult female house crickets closely follow daily activity cycles. However, the SMR in these individuals does not appear to have its own endogenous rhythm, nor is it independently affected by lighting conditions (Woodring & Clifford, 1986). Thus, it is not surprising that, in this study, the SMR of male house crickets did not vary with the time of day, or in response to ambient light levels. In contrast, several desert species of tenebrionid beetles vary their SMR by 75% or more over a daily cycle, regardless of lighting conditions (Bartholemew et al. 1985).

The weak, but consistent, increase in SMR over the
experiment's duration of nine weeks represents a paradoxical result. Changes in reproductive behaviour with seasonal light and temperature shifts are well documented in insects, including crickets (reviewed by Loher, 1989). Egg production significantly raises the oxygen consumption of outwardly 'inactive' females in A. domestica (Clifford & Woodring, 1986), and the daily production of spermatophores by male house crickets (McFarlane, 1968; Loher, 1974) may similarly increase their resting metabolism. It is possible that variation in environmental conditions during this study precipitated changes in male reproductive state, and thus metabolic rate. However, the individuals used in this study were maintained under a constant artificial light and temperature regimen and were unlikely to experience any consistent transition in conditions over the 9-week study. In addition, tested individuals were selected from laboratory stocks that bred throughout the year and did not exhibit strong seasonal differences in reproductive behaviour.

Alternative explanations for the observed effect of trial date on SMR include inadequate control of handling stress or digestive activity. Stress would be expected to increase the SMR, while recently fed individuals generally have a higher SMR than starved individuals (e.g. Tanaka & Ito, 1982). However, it is not clear why either stress or levels of digestive activity should have increased consistently over the course of the study.

Age

Irrespective of changes in aerobic metabolism due to body mass and trial date, mass-specific SMR was significantly lower in older adult male A. domestica than in young adult males. This result concurs with those from similar studies of humans and other mammals (see Introduction). For insects, physiological changes with age that possibly produce a decrease in SMR include decreases in mitochondrial efficiency, protein synthesis and flight muscle performance (reviewed by Sohal, 1985). If the observed age-related decrease in SMR does reflect a general deterioration in male physiological condition, we should expect males to decline in their ability to reproduce. In support of this hypothesis, when provided with receptive mates in the laboratory, male Gryllus bimaculatus showed reduced rates of copulation with increasing age (Simmons, 1988). However, females of several cricket species, including G. bimaculatus (Simmons & Zuk, 1992), prefer to associate with older males, both in laboratory and field environments (see Introduction). Thus, female preference for older males may occur in spite of their generally poorer physiological condition and its detrimental effect on characters such as their rate of spermatophore production (Simmons, 1988). This observation lends support to the hypothesis that age reflects the general genetic quality of males (Zuk, 1988; Simmons & Zuk, 1992) rather than a superior ability to advertise for, or court with, potential mates. However, whether females actually prefer to mate, and not just associate, with older males remains to be determined.

An alternative explanation for the age-associated decrease in SMR observed in this study is an age-associated decrease in activity not detected by the observer, e.g. subtle postural changes. Full et al. (1990) attribute the relatively high value they found for SMR in T. commodus to its habit of elevating the abdomen when at 'rest'. Test subjects in this study were considered active when in this posture and samples of VO2 during this period were excluded from analysis. Some brief, single movements of the antennae and mandibles were probably not detected but they would have to be very costly energetically in order to elevate the mean rate of oxygen consumption over the typical interval sampled. Both the absence of brief spikes in the continuous record of oxygen consumption rate and the only moderate energetic costs of tactics containing rapid mandible and antennal movements argue against this possibility (Huck, 1997b).

Finally, previous studies of insect metabolism have rarely controlled for factors other than body mass and temperature when measuring SMR (but see Armstrong & Mordue, 1985). An inconsistent definition of inactivity already confounds comparisons of SMR and factorial scopes across studies and taxa. The use of factorial scope values in evaluating relative energy expenditures on particular activities, such as locomotion (Bartholomew et al., 1981) or signalling (Burk, 1988), is only valid if inactive metabolic rates are determined under similar conditions. As this study demonstrates, controlling for the age of test subjects may be a simple and effective means of reducing error in measurements of SMR.

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