

Just drop it and run: the effect of limb autotomy on running distance and locomotion energetics of field crickets (*Gryllus bimaculatus*)

Patricia A. Fleming^{1,*} and Philip W. Bateman²

¹*School of Veterinary and Biomedical Sciences, Murdoch University, Murdoch, WA 6150, Australia and*

²*Department of Zoology and Entomology, University of Pretoria, Pretoria, 0002, South Africa*

*Author for correspondence (e-mail: T.Fleming@murdoch.edu.au)

Accepted 16 February 2007

Summary

This is the first study to examine the direct metabolic costs of autotomy, the voluntary shedding of an appendage as an escape mechanism, in invertebrates. We investigated the effects of limb autotomy upon endurance and metabolic cost of locomotion in the field cricket *Gryllus bimaculatus*. Compared with control (intact) crickets, animals that had autotomised a single hindlimb were slower, stopped more often, moved a shorter distance and expended more energy doing so. Both the cost of

locomotion (COT) and minimal cost of locomotion (MCOT) were significantly higher for autotomised animals. We compare these data with locomotion energetics of 36 other invertebrate species, and discuss the results in terms of the biomechanics of walking in crickets.

Key words: cost of transport, energy, insect, locomotion, metabolic rate, Orthoptera, running.

Introduction

Autotomy is an extreme response to predators, whereby an organism voluntarily sheds a limb or appendage to aid escape. While the benefits of this are obvious, and are reflected in the diversity of taxa in which it has evolved, the costs are more obscure. For instance, in the cricket *Gryllus bimaculatus*, loss of a leg through autotomy results in immediate costs in terms of escape speed and ability to jump during escape (Bateman and Fleming, 2005). In the cricket *Acheta domestica*, hindlimb autotomy similarly results in a significant reduction in escape speed and jumping ability, and therefore makes the animals more susceptible to predation by both lizards and mice (Bateman and Fleming, 2006a). An immediate cost in terms of reduced locomotion due to autotomy of an appendage has similarly been demonstrated for a number of other invertebrates; for example, reduced walking or running speed post-autotomy for harvestmen (Opiliones) (Guffey, 1999), spiders (Araneae) (Amaya et al., 2001; Apontes and Brown, 2005), and stick insects (Phasmatodea) (Carlberg, 1984), or a significant reduction in swimming speed after caudal lamellae autotomy in Odonata larvae (Burnside and Robinson, 1995; Gyssels and Stoks, 2005; McPeck et al., 1996; Robinson et al., 1991; Stoks, 1999). Crab swimming speed is also reduced by removal of a swimming leg (Juanes and Smith, 1995; Smith, 1995), and in starfish, arm loss significantly affects locomotory ability (Bingham et al., 2000; Slater and Lawrence, 1980).

Indirect assessment of the affects of autotomy upon energetic costs incurred through locomotion may be made by scrutiny of

the mechanisms of locomotion. For example, in the swimming bivalve *Limaria fragilis* (Mytiloidea), mantle tentacles contribute to swimming by a rowing motion (Donovan et al., 1994). Autotomy of the longest tentacles in these molluscs reduces clap distance by 13%, which the animals compensate for by clapping faster to maintain swimming speed (Donovan et al., 1994). This increased clap speed would therefore increase their metabolic expenditure in order to maintain swimming distance. As far as we are aware, however, the direct metabolic costs of locomotory impairment due to autotomy have not been measured for any invertebrate species.

Two important variables used to compare locomotor performance, both inter- and intraspecifically, are endurance capacity and metabolic energy costs (Full, 1987). The aim of the present study was to determine how autotomy of a hindleg affected the locomotory endurance for field crickets, *Gryllus bimaculatus*, and whether there was a measurable change in metabolic rate or cost of transport for these animals.

Materials and methods

Study animals

Gryllus bimaculatus (de Geer) (0.70±0.09 g) were obtained from colonies maintained at the Department of Zoology and Entomology, University of Pretoria. Colonies were kept under controlled temperature in cages (40 cm×40 cm×75 cm) with cardboard refuges and laying medium. Animals of known age were obtained by removal from the colony within 24 h post

adult moult and housed individually in 2 l plastic jars. Food (high protein cereal and fish food) and water were available *ad libitum* throughout this study. At the conclusion of these experiments, all animals were returned to the breeding colonies.

In this study, we examined two aspects of locomotory fitness in intact and autotomised crickets: endurance and respirometry.

Endurance

Our first measure of fitness was the distance run by an animal until it stopped and would move no further in response to stimulus (termed 'endurance'). For the study of endurance post-autotomy, a total of 60 crickets (30 male, 30 female) aged 7–14 days post adult eclosion were taken from a mixed-sex colony. They were moved to individual holding jars and held for 24 h prior to commencing experiments (we found that animals tested immediately after removal from large mixed-sex colonies demonstrated a significant increase in locomotion speed after 24 h of holding individually). On the experimental day, individuals were weighed (to 0.01 g) and measured for pronotum width (mm, using digital callipers). Animals were then placed into a circular arena of 1 m circumference and ~5 cm width. Crickets were timed upon introducing them to the arena. They were induced to run around the circumference of the arena by tapping a stick twice on the arena floor immediately behind the cricket whenever it stopped moving. Trials were stopped when two successive double-taps did not induce the cricket to move. The number of circuits (equivalent to distance in m), the number of taps (reflecting the number of stops the animal made), and the total time (s, measured with a stopwatch) were recorded and speed (m s^{-1}) subsequently calculated.

Animals were assigned to either autotomy or control (intact) treatments ($N=15$ for each treatment group for each sex) such that the speed and mass of individuals in each group were matched closely. Individuals in the autotomy group were induced to autotomise their right hindlimb (R_3) by grasping the leg with tweezers so that the animal had to autotomise its limb in order to escape. From previous data (Bateman and Fleming, 2005), we know that a hindleg weighs about $4.52 \pm 0.73\%$ ($N=66$) of the animals' body mass. Every individual was then re-run 24 h later. The change in distance run, speed and number of stops m^{-1} run were expressed as Day 2 values divided by Day 1 values for each individual. These three measurements (dependent variables) were each analysed for the effects of autotomy treatment and sex (independent factors), with body mass and pronotum width as covariates by analysis of covariance (ANCOVA).

Respirometry

Our second measure of locomotory fitness was the metabolic cost of transport incurred during escape running. The system employed in the present study therefore used a 'running tube' as a respirometry chamber, along which crickets ran back and forth at their own, and variable, speed; such a setup has been used successfully by other authors (Berrigan and Lighton,

1994; Duncan, 1999; Duncan and Lighton, 1997; Lighton and Duncan, 1995; Lighton and Feener, 1989; Lighton et al., 1993; Lipp et al., 2005). The running tube was made of a 1 m length of 40 mm diameter glass tubing, with a wax base that served two functions. The wax base occupied approximately one third of the internal volume; the final gas volume of the tube was therefore 800 ml. The wax base also allowed the crickets a flat surface upon which they could get purchase during running.

Measurements of CO_2 emission were carried out using a flow-through respirometry system (Sable Systems TR-2 from Sable Systems, Las Vegas, NV, USA). We present data for CO_2 emission rather than O_2 consumption because we were measuring CO_2 emission into a large volume (of our running tube) and stability and resolution of the LiCor analyser are superior to those of the best current O_2 analysers. The incurrent air stream was scrubbed of H_2O and CO_2 with silica gel and soda lime, respectively; air exiting the chamber was similarly scrubbed of H_2O before entering a CO_2 analyser (LiCor 6262, Lincoln, NE, USA). The gas analyser was then connected to a Sable Systems sub-sampler pump and mass flow controller. A flow rate of approximately 270 ml min^{-1} was maintained throughout the experiments, and temperature was relatively stable at about 21°C . Every 0.1 s, mass flow and CO_2 values ($\mu\text{mol mol}^{-1}$) were recorded on a PC (Datacan V, Sable Systems).

Measurements were made on 18 individual male crickets aged between 14 and 21 days post adult eclosion [we maintained constant ages since mass-specific metabolic rate has been shown to vary considerably with age in *Acheta domestica* (Hack, 1997)]. We only analysed males since females may be expected to show greater variability in metabolic rate due to different stages of egg production and are less able to increase metabolic activity during intense terrestrial exercise (Kolluru et al., 2004). Half of the crickets used had been induced to autotomise their right hindlimb 5 days prior to the experiment by grasping the leg with tweezers such that the animal had to autotomise its limb in order to escape. Measurements of autotomised and intact individuals were alternated during the experiment.

The experimental procedure was carried out as follows. A baseline CO_2 reading was recorded and then individuals were weighed (to 0.0001 g) and pronotum width measured (to 0.01 mm) before they were placed in the metabolic chamber. They were given at least 10 min to adjust to the chamber, during which time a small dark cloth was placed over the tube immediately above the cricket. This effectively confined the cricket to a length of about 10 cm. Although we could not observe any movements during this time, the cricket did not emerge from under the cloth and so was confined to this small area during this time. Readings from this time were used to estimate the resting metabolic rate of stationary crickets. After this, the animal was induced to move the length of the respiratory chamber by touching its back or hindlegs with a piece of card attached to a magnet controlled by a second magnet outside the chamber. The cricket was induced to move back and forth along the length of the chamber for at least

5–10 min (some animals struggled to keep moving for longer periods). The distance travelled (in m) and time spent moving (monitored with a stopwatch) were recorded in order to calculate average running speed (m s^{-1}).

The rates of mass-specific CO_2 production ($\text{ml s}^{-1} \text{kg}^{-1}$) were calculated for the initial rest phase ($R\dot{V}_{\text{CO}_2}$) and the activity bout ($A\dot{V}_{\text{CO}_2}$). Resting metabolic rate indicates the energetic costs of inactive subsistence, and were analysed for the effect of autotomy treatment (independent factor) by ANCOVA with body mass and pronotum width as covariates.

Crickets did not always reach a steady state of CO_2 production, often running faster and stronger at the commencement of exercise [similar to results for spiders on a treadmill (Schmitz, 2005)]. Therefore, $A\dot{V}_{\text{CO}_2}$ was calculated as the average of all data points between the start of the plateau (there was a steep increase in CO_2 upon commencement of activity, which then levelled out after about 3 min as the air within the running tube was replaced) to the end of the exercise period (whereupon CO_2 levels dropped immediately). Active metabolic rate data were analysed for the effect of autotomy treatment (independent factor) by ANCOVA, with body mass, pronotum width, mass-specific resting metabolic rate, and walking speed as covariates. The Cost of Transport (COT; calculated as $A\dot{V}_{\text{CO}_2}$ divided by walking speed) was analysed similarly. The slopes of $A\dot{V}_{\text{CO}_2}$ versus speed (the minimum cost of transport or MCOT) were compared for intact and autotomised animals by *t*-test (Zar, 1999).

All data are given as the mean \pm 1 s.d. The critical level for statistical analyses was set at $P < 0.05$ and statistical analyses were carried out using Statistica version 6.0 (StatSoft, 2001).

Results

Endurance

Autotomy significantly reduced the distance run (Fig. 1A, $F_{1,54}=6.27$, $P=0.015$) and average speed (Fig. 1B, $F_{1,54}=34.11$, $P < 0.001$) of crickets and also increased the number of stops m^{-1} run that they made (Fig. 1C, $F_{1,54}=21.35$, $P < 0.001$). There was no significant effect of sex for any of these analyses, and nor was there a significant effect of the covariates, body mass and pronotum width.

Respirometry

Resting metabolic rate ($R\dot{V}_{\text{CO}_2}$) was not significantly different between autotomised and intact animals (Fig. 2; $F_{1,14}=0.45$, $P=0.514$, the covariates body mass, $P=0.162$, and pronotum width, $P=0.677$, did not contribute significantly to $R\dot{V}_{\text{CO}_2}$). However, when the animals were active, despite being slower, on average, autotomised animals had significantly higher metabolic rates ($A\dot{V}_{\text{CO}_2}$) compared with intact control animals (Fig. 2, Table 1; $F_{1,12}=6.79$, $P=0.023$). Metabolic rate was significantly correlated with running speed, whilst body mass, pronotum width and resting metabolic rate ($R\dot{V}_{\text{CO}_2}$) did not significantly affect $A\dot{V}_{\text{CO}_2}$ (Table 1).

The slopes of $A\dot{V}_{\text{CO}_2}$ versus speed (MCOT) were significantly different for autotomised and control animals

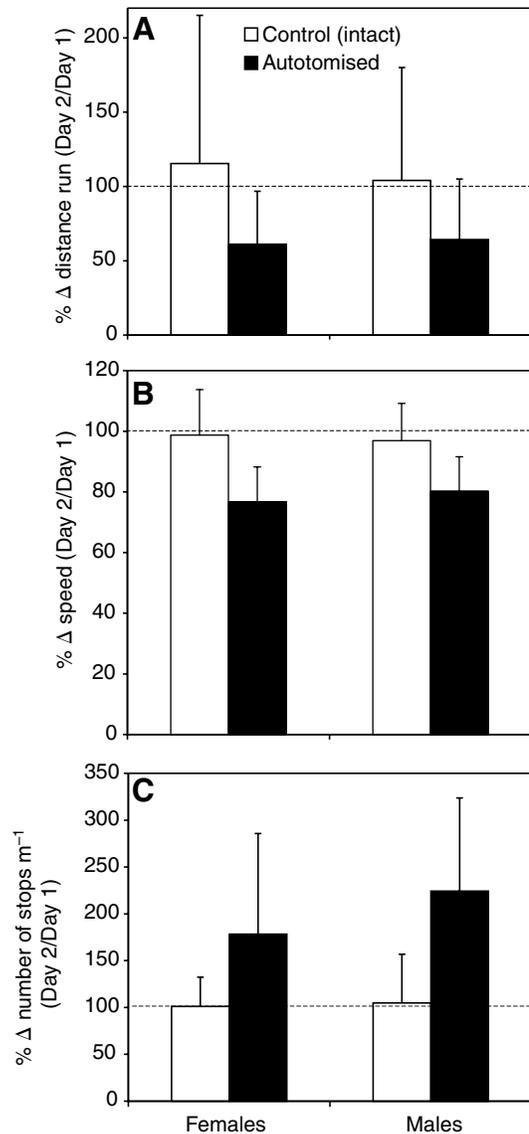


Fig. 1. Change in distance run (A), average speed of running (B) and average number of stops m^{-1} run (C) for intact (control) and autotomised male and female field crickets *Gryllus bimaculatus*. Values are means \pm 1 s.d. for $N=15$ individuals in each group.

(calculated from Fig. 2; $t_{14}=3.80$, $P < 0.001$). The cost of transport ($A\dot{V}_{\text{CO}_2}$ divided by speed; COT) was significantly affected by autotomy treatment, with COT values higher for autotomised animals, independently of walking speed (Table 2; $F_{1,12}=8.13$, $P=0.015$).

Discussion

Autotomy of a single hindleg significantly affects both the endurance and metabolic costs of locomotion in field crickets. Autotomised crickets ran a significantly shorter distance before they stopped responding to a stimulus, and stopped more frequently, compared with intact animals. Despite moving slower than intact animals, autotomised crickets had

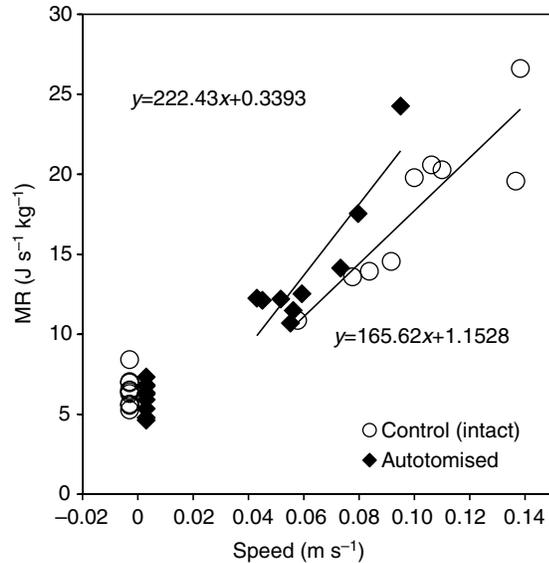


Fig. 2. The effect of autotomy on metabolic rate ($\text{J s}^{-1} \text{kg}^{-1}$, measured as \dot{V}_{CO_2} and converted to J [assuming an energy equivalent of $23.3 \text{ J ml CO}_2^{-1}$ (Duncan, 1999)] in 18 male field crickets *Gryllus bimaculatus*. Resting ($\text{R}\dot{V}_{\text{CO}_2}$; speed 0 m s^{-1}) and active ($\text{A}\dot{V}_{\text{CO}_2}$) metabolic rates (MR) were measured for each individual (two data points per individual are shown). Although there is a strong effect of speed on active metabolic rate, the effect of autotomy treatment (autotomised vs control/intact animals) was significant. Regression lines are drawn to fit active measurements.

significantly higher metabolic rates compared with intact, control animals. As far as we are aware, this is the first study that examines the direct metabolic costs of leg autotomy in an invertebrate. Here we discuss these results in terms of endurance, as well as the metabolic cost of locomotion.

There appears to be very little information on the locomotory endurance of arthropods. Most studies of locomotory energetics require that animals run only as far as required to achieve a stable metabolic state. None of the studies of Orthoptera we accessed discusses the endurance of the animal under examination. Blowflies ran >90% of the time (1.5 h) that they were in a recording chamber (Berrigan and Lighton, 1994). The same flies would walk continuously for 6–16 h ($\bar{x}=9.6 \text{ h}$), covering 465–814 m, during which time they would lose 50% of their body mass. Full examined endurance in ghost crabs (Full, 1987), and found that endurance time decreased as exercise speed increased, with small ($\bar{x}=2 \text{ g}$) animals showing the least stamina compared with larger ($\bar{x}=27 \text{ g}$ and $\bar{x}=71 \text{ g}$) animals. Our crickets demonstrated significant reduction in running endurance post-autotomy. Autotomised crickets moved an average of only $14.5 \pm 8.5 \text{ m}$ (range 3.75–35 m), compared with $26.6 \pm 19.6 \text{ m}$ (range 1–82 m) when intact.

Amongst arthropods, the energetic cost of pedestrian locomotion has been extensively studied in ants, cockroaches and beetles; a few studies have also been carried out on wasps, flies, spiders, mites and crabs (see Table 3 for details). As far as we are aware, only Full et al. have examined the energetic costs of locomotion in Orthoptera (Full et al., 1990). Some

Table 1. Results of ANCOVA examining the effect of autotomy treatment on active metabolic rate in 18 male field crickets *Gryllus bimaculatus*

Covariate	Effect on $\text{A}\dot{V}_{\text{CO}_2}$	
	<i>F</i>	<i>P</i>
Body mass (g)	0.57	0.465
Pronotum width (mm)	0.01	0.921
$\text{R}\dot{V}_{\text{CO}_2}$ ($\text{J s}^{-1} \text{kg}^{-1}$)	3.59	0.082
Speed (m s^{-1})	52.38	<0.001***
Autotomy treatment	6.79	0.023*

$\text{A}\dot{V}_{\text{CO}_2}$, Active metabolic rate ($\text{J s}^{-1} \text{kg}^{-1}$); $\text{R}\dot{V}_{\text{CO}_2}$, resting metabolic rate.
Data shown in bold contributed significantly to differences in $\text{A}\dot{V}_{\text{CO}_2}$.

Table 2. Results of ANCOVA examining the effect of autotomy treatment on the Cost of Transport for 18 male field crickets *Gryllus bimaculatus*

Covariate	Effect on COT	
	<i>F</i>	<i>P</i>
Body mass (g)	1.20	0.295
Pronotum width (mm)	0.27	0.610
$\text{R}\dot{V}_{\text{CO}_2}$ ($\text{J s}^{-1} \text{kg}^{-1}$)	4.52	0.055
Speed (m s^{-1})	<0.01	0.962
Autotomy treatment	8.13	0.015*

COT, Cost of Transport ($\text{J kg}^{-1} \text{m}^{-1}$); $\text{R}\dot{V}_{\text{CO}_2}$, resting metabolic rate.
Covariates analysed were body size (mass and pronotum width), resting metabolic rate ($\text{R}\dot{V}_{\text{CO}_2}$) and running speed. Only autotomy of a hindleg significantly affected COT (data shown in bold).

authors have assessed 'maximal metabolic rate' in a closed circuit system (e.g. shaking a sealed container containing the crickets with a uniform motion for a period of time, forcing the cricket to exercise vigorously) (Kolluru et al., 2004); there is, however, no quantification of activity level under this particular experimental setup. Hack examined the energetics of different male mating strategies in the house cricket *Acheta domestica*, comparing walking with calling behaviour (Hack, 1998); however, this study examined the costs 'per step or single cycle of movement of a single leg' when the animals were held in a small (47 ml) respiratory chamber; these data therefore do not allow for a comparison between walking speed and metabolic expenditure.

Oxygen consumption in the Australian field cricket *Teleogryllus commodus* ($0.95 \pm 0.07 \text{ g}$) was examined while running on a miniature treadmill (Full et al., 1990), and $\text{MCOT}=8.03 \text{ ml O}_2 \text{ g}^{-1} \text{ km}^{-1}$ oxygen consumption was recorded (equivalent to $0.161 \text{ J kg}^{-1} \text{ km}^{-1}$, using the authors' conversion of $1 \text{ ml O}_2=20.1 \text{ J}$). Our *G. bimaculatus* ($0.70 \pm 0.09 \text{ g}$) did not achieve a steady state of locomotion, with a brief burst of high-speed running followed by slower movement. Nevertheless, the cost of locomotion in our animals

Table 3. Comparative data for the energetics of locomotion in a range of arthropods

Group	Species	Technique	Temperature (°C)	Body mass (g)	Active MR ($\text{J s}^{-1} \text{kg}^{-1}$) as a function of speed v (m s^{-1})			Reference
					Equation	N	r^2	
Crickets	<i>Gryllus bimaculatus</i>	RT	21	0.70±0.09	165.6v+1.2*	14 intact	0.80	This study
		T	23.5	0.95±0.07	222.4v+0.3*	9 autotomised	0.80	This study
Ants	<i>Teleogryllus commodus</i>	T	28	0.031	161.4v+6.1	60	0.54	(Full and Tullis, 1990a)
	<i>Atta colombica</i>	T	28	0.031	187.3v+3.7	11	0.64	(Lighton et al., 1987)
	<i>Camponotus</i> sp.	RT	25–30?	0.012±0.004	122.7v+3.3*	289	0.91	(Lipp et al., 2005)
	<i>Formica fusca</i>	RT [†]	20–25	0.0047±0.0010	700.9v+?*	6	0.93	(Jensen and Holm-Jensen, 1980)
	<i>Formica rufa</i>	RT [†]	20–25	0.0091±0.0017	707.1v+?*	4	0.79 [§]	(Jensen and Holm-Jensen, 1980)
	<i>Messor capitatus</i>	RT			No correlation between speed and the cost of running			(Nielson and Baroni-Urbani, 1990)
	<i>Leptogenys attenuata</i>	RT	25	0.0054±0.0002 (13)	189.0v+4.0*	9		(Duncan and Crewe, 1993)
	<i>Leptogenys nitida</i>	RT	20	0.0017±0.0003 (40)	189.1v+2.5*	6		(Duncan and Crewe, 1993)
	<i>Leptogenys nitida</i>	RT	25	0.0017±0.0003 (40)	207.4v+3.3*	14		(Duncan and Crewe, 1993)
	<i>Leptogenys nitida</i>	RT	30	0.0017±0.0003 (40)	300.5v+1.8*	10		(Duncan and Crewe, 1993)
<i>Leptogenys nitida</i>	RT	35	0.0017±0.0003 (40)	186.2v+5.4*	10		(Duncan and Crewe, 1993)	
<i>Leptogenys schwabi</i>	RT	20	0.0085±0.0007 (43)	260.7v+0.7*	10		(Duncan and Crewe, 1993)	
<i>Leptogenys schwabi</i>	RT	25	0.0085±0.0007 (43)	186.7v+2.9*	10		(Duncan and Crewe, 1993)	
<i>Leptogenys schwabi</i>	RT	30	0.0085±0.0007 (43)	277.3v+2.7*	11		(Duncan and Crewe, 1993)	
<i>Leptogenys schwabi</i>	RT	35	0.0085±0.0007 (43)	170.6v+4.7*	12		(Duncan and Crewe, 1993)	
<i>Megaponera foetens</i> minors	RT	25	0.0124 (18)	121.5v+5.4*	18		(Duncan, 1995)	
<i>Megaponera foetens</i> majors	RT	25	0.0404 (16)	122.7v+3.3*	16		(Duncan, 1995)	
<i>Myrmecocystus mendax</i>	RT	40	0.006±0.002 (16)*	158.2v+5.6*	16	0.54	(Duncan and Lighton, 1994)	
<i>Myrmecocystus mexicanus</i>	RT	30	0.014±0.004 (16)*	104.5v+1.7*	16	0.50	(Duncan and Lighton, 1994)	
<i>Pachycondyla berthoudi</i>	RT	25	0.027±0.002	165.9v+1.2	32	0.33	(Duncan, 1999)	
<i>Paraponera clavata</i>	T	28	0.019±0.015	212.9v+0.1	6	0.56	(Fewell et al., 1996)	
<i>Pogonomyrmex rugosus</i>	RT and T	34–43	0.017	188.2v+?*	30		(Lighton and Feener, 1989)	
Wasps	<i>Dasyneura gloriosa</i>	RT	30	0.076±0.023	168.9v+3.3*	6	0.38, $P<0.001$	(Duncan and Lighton, 1997)
Beetles	<i>Anthia fabricii</i>	T	22	2.25±0.07	40.1v+2.8	x	0.76	(Lighton, 1985)
	<i>Calosoma affine</i>	T	23.5	0.62±0.08	93.1v+1.5	17	0.71	(Full and Tullis, 1990a)
	<i>Onymacris plana</i>	T	35	0.691	191.6v+2.6 [¶]	16		(Bartholomew et al., 1985)
	<i>Pachysoma hippocrates</i>	T	22	3.05±0.21	88.7v+0.6	2	0.63	(Lighton, 1985)
	<i>Physadesmia globosa</i>	T	35	0.652	39.1v+9.8	9	ns	(Bartholomew et al., 1985)
	<i>Physosierma cribripes</i>	T	35	1.226	60.2v+2.9	1	0.99	(Bartholomew et al., 1985)
	<i>Psammodes striatus</i>	T	22	2.89±0.31	31.1v+1.2	5	0.53	(Lighton, 1985)

Table 3. Continued

Group	Species	Technique	Temperature (°C)	Body mass (g)	Active MR ($\text{J s}^{-1} \text{kg}^{-1}$) as a function of speed v (m s^{-1})			Reference
					Equation	N	r^2	
Cockroaches	<i>Blaberus discoidalis</i>	T	25	4.08±0.76 (8)	57.8v+2.7	8	0.79	(Herreid and Full, 1984)
	<i>Blaberus discoidalis</i>	T	15	4.15	116.3v+2.6	18	0.65	(Full and Tullis, 1990a)
	<i>Blaberus discoidalis</i>	T	23	4.15	102.5v+3.9	43	0.83	(Full and Tullis, 1990a)
	<i>Blaberus discoidalis</i>	T	34	4.15	120.0v+3.9			(Full and Tullis, 1990a)
	<i>Blaberus giganteus</i>	T	25–27	4.33±0.81	46.6v+0.2	5	0.93	(Bartholomew and Lighton, 1985)
	<i>Eublaberus posticus</i>	T	25	2.20±0.32 (3)	154.5v+0.3	3	0.75	(Herreid and Full, 1984)
	<i>Gromphadorhina chopardi</i>	T	25	3.4	50.7v+1.4		0.76	(Herreid and Full, 1984)
	<i>Gromphadorhina portentosa</i>	T	24	5.2±0.8 (10)	91.7v+2.3	30		(Herreid et al., 1981a; Herreid et al., 1981b)
								(Full and Tullis, 1990b)
Flies	<i>Periplaneta americana</i>	T	24	0.78±0.09	126.2v+2.0	16	0.82	(Full and Tullis, 1990a)
	<i>Periplaneta americana</i>	T	23.5	0.90±0.11	169.8v+0.9	30	0.84	(Full and Tullis, 1990a)
	<i>Periplaneta americana</i>	T	25	0.73±0.084 (15)	183.2v+1.6	29	0.88	(Herreid and Full, 1984)
Flies	<i>Protophormia terraenovae</i>	RT	30	0.043	254.0v +11.8*	19		(Berrigan and Lighton, 1994)
Spiders	<i>Marpissa muscosa</i>	T	20	0.03±0.009	437.7v+4.1*	30		(Schmitz, 2005)
	<i>Myrmecopygus rettenmeyeri</i>	T	28	0.022±0.006	159.6v+11.2*	5	0.92	(Lighton and Gillespie, 1989)
	<i>Pardosa lugubris</i>	T	20	0.031±0.009	138.0v+5.6*	24		(Schmitz, 2005)
	<i>Tarantula</i> (subF Theraphosinae)	T	24	12.7	8.0v+0.6	7		
								(Lighton and Duncan, 1995)
Mites	<i>Dinorhombium magnificum</i>	RT	24	0.032±0.015	130.5v+1.1*	10		
Crabs	<i>Ocypode quadrata</i>	T	24	2.1±0.58 (5)	69.5v+2.3	15	0.67	(Full, 1987)
	<i>Ocypode quadrata</i>	T	24	26.9±0.74 (5)	16.0v+0.9	15	0.76	(Full, 1987)
	<i>Ocypode quadrata</i>	T	24	70.9±3.49 (5)	8.4v+1.4	21	0.42	(Full, 1987)

For *Gryllus bimaculatus* (this study), the data are presented for 14 trials of intact males only. Although a linear equation described the relationship between \dot{V}_{CO_2} and walking speed well ($r^2=0.6697$), a slightly better relationship was gained using a polynomial regression ($r^2=0.7057$); the linear relationship between metabolic cost of transport and walking speed is, however, presented to be consistent with the literature (e.g. Full et al., 1990; Herreid et al., 1981a; Lighton and Feener, 1989).

All values were converted to metabolic rate in $\text{J s}^{-1} \text{kg}^{-1}$ [assuming a respiratory quotient, RQ, of 0.8 and an energy equivalent of 23.3 J ml CO_2^{-1} (Duncan, 1999), unless the authors specifically measured RQ], and speed in m s^{-1} . Sample sizes for body mass, where available, are given in parentheses; r^2 values have been given wherever they were available; values have been converted to means ± 1 s.d.

RT indicates studies that used a running tube, T indicates the use of a miniature treadmill.

*Values converted from \dot{V}_{CO_2} .

†A circular running tube was used, but the ants were encouraged to run at a fixed pace by a rotating steel ball (this data was analysed as 'treadmill' for statistical comparison).

‡Excluding two outliers.

§Above $\sim 0.13 \text{ m s}^{-1}$ the animals did not increase \dot{V}_{O_2} significantly.

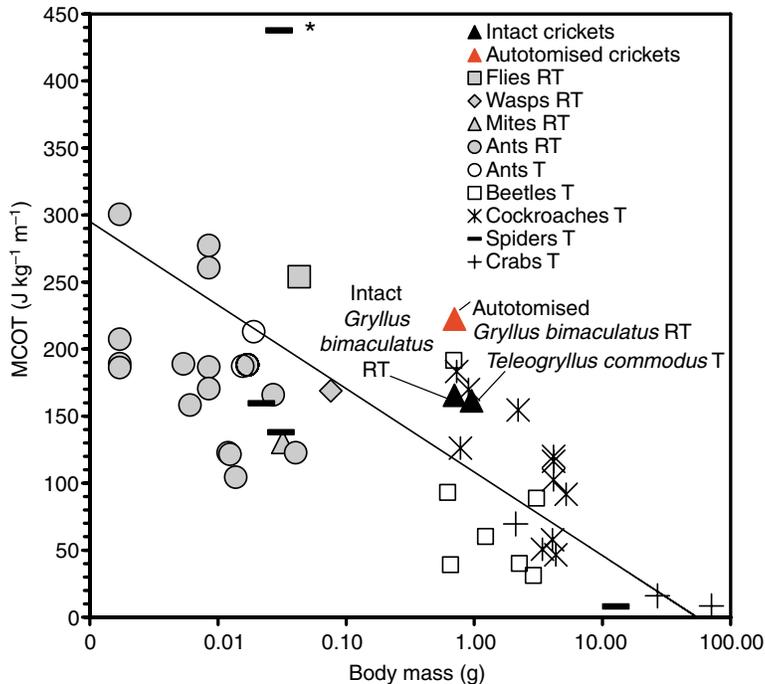


Fig. 3. The minimum cost of transport (MCOT) compared with body mass for data listed in Table 3. RT indicates studies that used a running tube; T indicates the use of a miniature treadmill. The regression line is fitted to all species and is statistically significant ($r^2=0.56$, $F_{1,39}=25.40$, $P<0.001$). -* indicates data for *Marpissa muscosa*, which is discussed in the text.

was remarkably similar to that for *T. commodus*, at $0.178 \pm 0.018 \text{ J kg}^{-1} \text{ km}^{-1}$ for intact and $0.230 \pm 0.034 \text{ J kg}^{-1} \text{ km}^{-1}$ for autotomised *G. bimaculatus*.

Because there is so little data available for Orthoptera, we have reviewed available data for other arthropods (Table 3). With very few exceptions, these data invariably indicate a marked rise in metabolic expenditure with increased locomotory speeds. Because every study is carried out under its own experimental conditions, particularly temperature, we could not expect the metabolic rates of poikilotherms to remain consistent between studies. The elevation of the lines drawing the relationship between metabolic rate and speed would therefore vary markedly between studies (Lighton and Feener, 1989). However the slopes of the lines drawn (MCOT values) have been demonstrated to be markedly resilient to variation in temperature (e.g. Full and Tullis, 1990a; Lighton and Feener, 1989; Weier et al., 1995). In Fig. 3 the MCOT values for each study are plotted against body mass. MCOT scales inversely with body mass, and is therefore higher for small animals (Lighton and Feener, 1989).

The data for *T. commodus* and *G. bimaculatus* reveal that these crickets have similar MCOT to other species of similar mass and do not appear to be exceptional in regard to their normal energetics, sitting very close to the regression line for these data (Fig. 3). However when they have autotomised a hindleg, *G. bimaculatus* demonstrate significantly higher MCOT values than intact animals. In this study we only

examined the affect of autotomy of a single leg. An estimated 29% of males and 38% of females in a field population of *Gryllus bimaculatus* were missing limbs, with 18% of males and 13% of females missing more than one leg (Bateman and Fleming, 2005). We would anticipate further increases in the energetic cost of locomotion with additional leg loss, since the effects upon the biomechanics of walking become more pronounced with additional leg loss (Hughes, 1957).

Autotomised crickets are not able to walk as fast as intact animals, and have increased metabolic rates; their COT and MCOT values are significantly higher than for intact crickets. Such a result suggests that loss of a leg interferes with the walking biomechanics in these animals, since removal of a leg results in the remaining legs having to function under altered conditions (Hughes, 1957). The mechanisms used by a species to move significantly affect the efficiency of such locomotion (Full et al., 1990).

Crickets are likely to use the alternating tripod gait when moving fast (Delcomyn, 1981). This gait 'ensures that at least three legs are in contact with the walking surface at all times, and that the insect's centre of gravity is always within the base of support formed by the stationary legs' [(Delcomyn, 1981), p. 105]. This gait is altered upon autotomy of a leg. Furthermore, 'the proportion of time that a leg spends off the ground during each step increases as the speed of the animal increases' [(Delcomyn, 1981), p. 110], suggesting that the costs of autotomy would be most evident during faster paces, as we found.

The effects of limb amputation on locomotion (reviewed by Delcomyn, 1981) have been examined in cockroaches (Delcomyn, 1971; Hughes, 1957), beetles (Wilson, 1966) and stick insects (Graham, 1977). Loss of even a single limb in cockroaches results in a significant alteration to the posture of the remaining limbs (Hughes, 1957). Loss of a hindlimb results in shortened stride of the remaining hindlimb, which is held closer into the body and is apparently 'dragged' (so that it exerted little propulsive thrust), the middle legs are held closer to the body, and the front and middle legs on the amputated side are retracted farther back than normal (Hughes, 1957). The loss of propulsion and balance experienced upon loss of a leg, coupled with increased proportion of body mass supported and altered coordination, is therefore likely to account for the greater costs of locomotion experienced by autotomised animals.

A number of authors have suggested that various spiders and harvestmen may have 'spare legs', with individuals appearing to suffer minimal costs from the loss of a limb or two (Brueseke et al., 2001; Brueseke et al., 1999; Johnson and Jakob, 1999) (but see Amaya et al., 2001; Apontes and Brown, 2005). This hypothesis might predict that the animal has excellent walking biomechanics, such that the loss of a single leg impedes natural movements only minimally. It might, therefore, be expected that

such spiders have a low MCOT. Consistent with this, a tarantula, the wolf spider *Pardosa lugubris* (Lycosidae) and *Myrmecotypus rettenmeyeri* (Clubionidae), show MCOT values that are small for their respective body masses (Fig. 3) (Herreid et al., 1981b; Lighton and Gillespie, 1989; Schmitz, 2005). On the other hand, data for *Marpissa muscosa* (Salticidae) indicates that these jumping spiders have a very high MCOT (in Fig. 3) and pay a heavy metabolic cost for faster locomotion (Schmitz, 2005). This may be due to unique locomotion mechanics in these spiders, which jump rather than walk. Given the 'spare leg' hypothesis for some arachnids, it would be very informative to compare the MCOT values for more spider species, and examine the effects of autotomy upon these costs.

Despite the benefits of losing a leg in order to escape a predator, there are nevertheless many costs of leg autotomy incurred by crickets. In this study, we found that autotomy of a single hindlimb significantly reduced endurance and also increased the metabolic costs of locomotion for these animals. Both compromised endurance and energetics would contribute to an increased likelihood of failing to survive a subsequent predatory encounter. Furthermore, the energetic costs of locomotion may also contribute to alterations in specific mating behaviours, which we have demonstrated are affected by limb autotomy (e.g. Bateman and Fleming, 2005; Bateman and Fleming, 2006b; Bateman and Fleming, 2006c).

One particularly important consideration for autotomised crickets may be a trade-off between the metabolic costs of calling (e.g. Hack, 1998; Hoback and Wagner, 1997) and locomotion in order to secure a mate. For intact crickets, locomotion may incur expenses comparable to those of calling. For example, in the house cricket, *Acheta domestica*, high pulse rate chirping is equally as energetically expensive as walking (low pulse rate chirping is an order of magnitude less energetically expensive than walking, although less effective at attracting mates) (Hack, 1998). However, if the costs of locomotion are increased (e.g. by autotomy of a leg or two), then calling may become significantly more advantageous. Crickets may therefore have to make energetic trade-offs that impact on lifetime reproductive success in response to autotomy of a limb. These trade-offs due to energetic costs of calling and locomotion may reflect the reduced ability of autotomised males to compete with intact males for mates (Bateman and Fleming, 2005).

A second trade-off may be balancing the amount of time spent walking to find a mate *versus* remaining stationary. Many cricket males sing from burrows to reduce predation risk and to allow sequestering of females (Simmons, 1986a; Simmons, 1986b). However, small male *Scapsipedus meridianus* that are unable to obtain a burrow sing less and move more to avoid predation than males who have a burrow from which to sing (Bateman, 2000); these crickets would therefore accrue multiple negative impacts due to forced locomotion (if they experience similar higher costs of locomotion as *G. bimaculatus* post limb autotomy). Also, females responding to male call may put less effort into their phonotaxis if they are missing a limb and therefore incurring an increase in metabolic

cost of transport compared with intact females. A reduction in locomotory behaviour would presumably be to the detriment of reproductive activity.

Thirdly, both males and females may incur increased energetic costs of movement when foraging if they have autotomised a limb. In male *Gryllus campestris*, acoustic signalling is condition-dependent, with well-fed crickets being able to sing more (Holzer et al., 2003). For female gryllid crickets, egg production is also affected by nutritional status: female black-horned tree crickets (*Oecanthus nigricornis*) that receive large nuptial gifts lay more eggs (Brown et al., 1996).

Overall, therefore, due to the increased costs of locomotion after they have autotomised a limb, crickets may have to shun potentially dangerous situations, avoid metabolically costly activities, and may have reduced feeding and therefore fecundity. But at least they are still alive.

We would like to thank Frances Duncan for her invaluable help during this project. Thanks also to Sue Nicolson for access to equipment.

References

- Amaya, C. C., Klawinski, P. D. and Formanowicz, D. R. (2001). The effects of leg autotomy on running speed and foraging ability in two species of wolf spider (Lycosidae). *Am. Midl. Nat.* **145**, 201-205.
- Apontes, P. and Brown, C. A. (2005). Between-sex variation in running speed and a potential cost of leg autotomy in the wolf spider *Pirata sedentarius*. *Am. Midl. Nat.* **154**, 115-125.
- Bartholomew, G. A. and Lighton, J. R. B. (1985). Ventilation and oxygen consumption during rest and locomotion in a tropical cockroach, *Blaberus giganteus*. *J. Exp. Biol.* **118**, 449-454.
- Bartholomew, G. A., Lighton, J. R. B. and Louw, G. N. (1985). Energetics of locomotion and patterns of respiration in tenebrionid beetles from the Namib desert. *J. Comp. Physiol. B* **155**, 155-162.
- Bateman, P. W. (2000). Burrow residency, access to females and body size in male *Scapsipedus meridianus* (Orthoptera: Gryllidae; Gryllinae, Otte & Cade). *J. Orthoptera Res.* **9**, 27-29.
- Bateman, P. W. and Fleming, P. A. (2005). Direct and indirect costs of limb autotomy in field crickets *Gryllus bimaculatus*. *Anim. Behav.* **69**, 151-159.
- Bateman, P. W. and Fleming, P. A. (2006a). Increased susceptibility to predation for autotomized house crickets (*Acheta domestica*). *Ethology* **112**, 670-677.
- Bateman, P. W. and Fleming, P. A. (2006b). Sex and the single (-eared) female: leg function, limb autotomy and mating history trade-offs in field crickets (*Gryllus bimaculatus*). *Biol. Lett.* **2**, 33-35.
- Bateman, P. W. and Fleming, P. A. (2006c). Sex, intimidation and severed limbs: the effect of simulated predator attack and limb autotomy on calling and emergence behaviour in the field cricket *Gryllus bimaculatus*. *Behav. Ecol. Sociobiol.* **59**, 674-681.
- Berrigan, D. and Lighton, J. R. B. (1994). Energetics of pedestrian locomotion in adult male blowflies, *Protophormia terranova* (Diptera: Calliphoridae). *Physiol. Zool.* **67**, 1140-1153.
- Bingham, B. L., Burr, J. and Wounded Head, H. (2000). Causes and consequences of arm damage in the sea star *Leptasterias hexactis*. *Can. J. Zool.* **78**, 596-605.
- Brown, W. D., Wideman, J., Andrade, M. C. B., Mason, A. C. and Gwynne, D. T. (1996). Female choice for an indicator of male size in the song of the black-horned tree cricket, *Oecanthus nigricornis* (Orthoptera: Gryllidae: Oecanthinae). *Evolution* **50**, 2400-2411.
- Brueseke, M., Rypstra, A., Walker, S. and Persons, M. (2001). Leg autotomy in the wolf spider *Pardosa milvina*: a common phenomenon with few apparent costs. *Am. Midl. Nat.* **146**, 153-160.
- Burnside, C. A. and Robinson, J. V. (1995). The functional morphology of caudal lamellae in Coenagrionid (Odonata, Zygoptera) damselfly larvae. *Zool. J. Linn. Soc.* **114**, 155-171.

- Carlberg, U.** (1984). Walking velocity in first instar nymphs of *Extatosoma tiaratum* (MacLeay) (Insecta: Phasmoda). *Zool. Anz.* **212**, 223-225.
- Delcomyn, F.** (1971). The effect of limb amputation on locomotion in the cockroach *Periplaneta americana*. *J. Exp. Biol.* **54**, 453-469.
- Delcomyn, F.** (1981). Insect locomotion on land. In *Locomotion and Energetics in Arthropods* (ed. C. F. Herreid and C. R. Fournier), pp. 103-125. New York: Plenum Press.
- Donovan, D. A., Elias, J. P. and Baldwin, J.** (1994). Swimming behavior and morphometry of the file shell *Limaria fragilis*. *Mar. Freshw. Behav. Physiol.* **37**, 7-16.
- Duncan, F. D.** (1995). A reason for division of labor in ant foraging. *Naturwissenschaften* **82**, 293-296.
- Duncan, F. D.** (1999). The ponerine ant *Pachycondyla (=Ophthalmopone) berthoudi* Forel carries loads economically. *Physiol. Biochem. Zool.* **72**, 71-77.
- Duncan, F. D. and Crewe, R. M.** (1993). A comparison of the energetics of foraging of three species of *Leptogenys* (Hymenoptera, Formicidae). *Physiol. Entomol.* **18**, 372-378.
- Duncan, F. D. and Lighton, J. R. B.** (1994). The burden within: the energy cost of load carriage in the honeypot ant, *Myrmecocystus*. *Physiol. Zool.* **67**, 190-203.
- Duncan, F. D. and Lighton, J. R. B.** (1997). Discontinuous ventilation and energetics of locomotion in the desert-dwelling female mutillid wasp, *Dasymutilla gloriosa*. *Physiol. Entomol.* **22**, 310-315.
- Fewell, J. H., Lighton, J. R. B. and Harrison, J. F.** (1996). Energetics of foraging in the giant tropical ant *Paraponera clavata*. *Oecologia* **105**, 419-427.
- Full, R. J.** (1987). Locomotion energetics of the ghost crab. I. Metabolic cost and endurance. *J. Exp. Biol.* **130**, 137-153.
- Full, R. J. and Tullis, A.** (1990a). Capacity for sustained terrestrial locomotion in an insect: energetics, thermal dependence, and kinematics. *J. Comp. Physiol. B* **160**, 573-581.
- Full, R. J. and Tullis, A.** (1990b). Energetics of ascent: insects on inclines. *J. Exp. Biol.* **149**, 307-317.
- Full, R. J., Zuccarello, D. A. and Tullis, A.** (1990). Effect of variation in form on the cost of terrestrial locomotion. *J. Exp. Biol.* **150**, 233-246.
- Graham, D.** (1977). The effect of amputation and leg restraint on the free walking coordination of the stick insect *Carausius morosus*. *J. Comp. Physiol.* **116**, 91-116.
- Guffey, C.** (1999). Costs associated with leg autotomy in the harvestmen *Leiobunum nigripes* and *Leiobunum vittatum* (Arachnida: Opiliones). *Can. J. Zool.* **77**, 824-830.
- Gyssels, F. G. M. and Stoks, R.** (2005). Threat-sensitive responses to predator attacks in a damselfly. *Ethology* **111**, 411-423.
- Hack, M. A.** (1997). The effects of mass and age on standard metabolic rate in house crickets. *Physiol. Entomol.* **22**, 325-331.
- Hack, M. A.** (1998). The energetics of male mating strategies in field crickets (Orthoptera: Gryllinae: Gryllidae). *J. Insect Behav.* **11**, 853-867.
- Herreid, C. F. and Full, R. J.** (1984). Cockroaches on a treadmill: aerobic running. *J. Insect Physiol.* **30**, 395-403.
- Herreid, C. F., Full, R. J. and Prawel, D. A.** (1981a). Energetics of cockroach locomotion. *J. Exp. Biol.* **94**, 189-202.
- Herreid, C. F., Prawel, D. A. and Full, R. J.** (1981b). Energetics of running cockroaches. *Science* **212**, 331-333.
- Hoback, W. W. and Wagner, W. E. J.** (1997). The energetic costs of calling in the variable field cricket, *Gryllus lineaticeps*. *Physiol. Entomol.* **22**, 286-290.
- Holzer, B., Jacot, A. and Brinkhof, M. W. G.** (2003). Condition-dependent signaling affects male sexual attractiveness in field crickets, *Gryllus campestris*. *Behav. Ecol.* **14**, 353-359.
- Hughes, G. M.** (1957). The coordination of insect movements: II. The effect of limb amputation and the cutting of commissures in the cockroach (*Blattella orientalis*). *J. Exp. Biol.* **34**, 306-333.
- Jensen, T. F. and Holm-Jensen, I.** (1980). Energetic cost of running in workers of three ant species, *Formica fusca* L., *Formica rufa* L., and *Camponotus herculeanus* L. (Hymenoptera, Formicidae). *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* **137**, 151-156.
- Johnson, S. and Jakob, E.** (1999). Leg autotomy in a spider has minimal costs in competitive ability and development. *Anim. Behav.* **57**, 957-965.
- Juanes, F. and Smith, L.** (1995). The ecological consequences of limb damage and loss in decapod crustaceans: a review and prospectus. *J. Exp. Mar. Biol. Ecol.* **193**, 197-223.
- Kolluru, G. R., Chappell, M. A. and Zuk, M.** (2004). Sex differences in metabolic rates in field crickets and their dipteran parasitoids. *J. Comp. Physiol. B* **174**, 641-648.
- Lighton, J. R. B.** (1985). Minimum costs of transport and ventilatory patterns in three African beetles. *Physiol. Zool.* **58**, 390-399.
- Lighton, J. R. B. and Duncan, F. D.** (1995). Standard and exercise metabolism and the dynamics of gas exchange in the giant red velvet mite, *Dinothrombium magnificum*. *J. Insect Physiol.* **41**, 877-884.
- Lighton, J. R. B. and Feener, D. H.** (1989). A comparison of energetics and ventilation of desert ants during voluntary and forced locomotion. *Nature* **342**, 174-175.
- Lighton, J. R. B. and Gillespie, R. G.** (1989). The energetics of mimicry: the cost of pedestrian transport in a formicine ant and its mimic, a clubionid spider. *Physiol. Entomol.* **14**, 173-177.
- Lighton, J. R. B., Bartholomew, G. A. and Feener, D. H.** (1987). Energetics of locomotion and load carriage and a model of the energy cost of foraging in the leaf-cutting ant *Atta colombica*. *Physiol. Zool.* **60**, 524-537.
- Lighton, J. R. B., Weier, J. A. and Feener, D. H.** (1993). The energetics of locomotion and load carriage in the desert harvester ant, *Pogonomyrmex rugosus*. *J. Exp. Biol.* **181**, 49-61.
- Lipp, A., Wolf, H. and Lehmann, F.-O.** (2005). Walking on inclines: energetics of locomotion in the ant *Camponotus*. *J. Exp. Biol.* **208**, 707-719.
- McPeck, M. A., Schrot, A. K. and Brown, J. M.** (1996). Adaptation to predators in a new community: swimming performance and predator avoidance in damselflies. *Ecology* **77**, 617-629.
- Nielson, M. G. and Baroni-Urbani, C.** (1990). Energetics and foraging behavior of the European seed harvesting ant *Messor capitatus*. I. Respiratory metabolism and energy consumption of unloaded and loaded workers during locomotion. *Physiol. Entomol.* **15**, 441-448.
- Robinson, J. V., Hayworth, D. A. and Harvey, M. B.** (1991). The effect of caudal lamellae loss on swimming speed of the damselfly *Argia moesta* (Hagen) (Odonata, Coenagrionidae). *Am. Midl. Nat.* **125**, 240-244.
- Schmitz, A.** (2005). Spiders on a treadmill: influence of running activity on metabolic rates in *Pardosa lugubris* (Araneae, Lycosidae) and *Marpissa muscosa* (Araneae, Salticidae). *J. Exp. Biol.* **208**, 1401-1411.
- Simmons, L. W.** (1986a). Female choice in the field cricket *Gryllus bimaculatus* (De Geer). *Anim. Behav.* **34**, 1463-1470.
- Simmons, L. W.** (1986b). Inter-male competition and mating success in the field cricket *Gryllus bimaculatus* (De Geer). *Anim. Behav.* **34**, 567-579.
- Slater, A. and Lawrence, J. M.** (1980). The effect of arm loss on feeding and growth rates in *Luidia clathrata*. *Fla. Sci.* **43**, 16.
- Smith, L. D.** (1995). Effects of limb autotomy and tethering on juvenile blue crab survival from cannibalism. *Mar. Ecol. Prog. Ser.* **116**, 65-74.
- StatSoft** (2001). STATISTICA (data analysis software system). www.statsoft.com.
- Stoks, R.** (1999). The effect of lamellae autotomy and sexual size dimorphism on startle-response performance in larvae of a lepidopteran damselfly (Odonata). *J. Zool. Lond.* **247**, 269-273.
- Weier, J. A., Feener, D. H. and Lighton, J. R. B.** (1995). Inter-individual variation in energy cost of running and loading in the seed-harvester ant, *Pogonomyrmex maricopa*. *J. Insect Physiol.* **41**, 321-327.
- Wilson, D. M.** (1966). Insect walking. *Annu. Rev. Entomol.* **11**, 103-122.
- Zar, J. H.** (1999). *Biostatistical Analysis*. Upper Saddle River: Prentice Hall.