

INEXPENSIVE LOAD CARRYING BY RHINOCEROS BEETLES

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Summary

These experiments determined the magnitude of loads that rhinoceros beetles (Scarabaeidae) can carry and also the metabolic energy required for carrying loads. I hypothesized that, like many other animals, these beetles would have metabolic rates in direct proportion to the total load (body mass plus added mass). Eight beetles (*Xylorctes thestalus*) walked at 1 cm s^{-1} on a motorized treadmill enclosed in a respirometer. The beetles could sustain this speed with loads of more than 30 times their body mass. In

addition to being strong, these beetles carry loads with remarkable economy. The metabolic cost of moving a gram of additional load was more than five times cheaper than that of moving a gram of body mass. This phenomenon cannot be explained by conventional models that link the biomechanics and metabolic energy cost of locomotion.

Key words: locomotion, energetics, biomechanics, load carrying, rhinoceros beetle, *Xylorctes thestalus*.

Introduction

When an animal walks or runs, the muscles of the limbs must exert force to support the weight of the body plus any added load. The muscles must also perform some mechanical work to lift the center of mass vertically against gravity, to accelerate the body in the fore–aft direction and also to accelerate the limbs relative to the center of mass. The metabolic energy consumed by a walking or running animal is related to the magnitude and rate of isometric force development as well as the mechanical work performed by muscles, but it is not yet clear what portion of the energy should be attributed to each of these factors (Kram and Taylor, 1990; Alexander, 1991). In any case, carrying extra loads normally requires the muscles both to exert higher forces and to perform more mechanical work and thus normally the rate of metabolic energy consumption increases.

When a walking or running mammal carries an extra load, its metabolic rate increases in direct proportion to the extra load expressed as a percentage of body mass (Taylor *et al.* 1980). For example, at any particular speed, when a 70 kg person carries a load of 14 kg (=20% of body mass), their metabolic rate increases by 20%. This same pattern applies to a variety of other mammals including horses, dogs and rats (Taylor *et al.* 1980).

When it comes to carrying loads, rhinoceros beetles (Scarabaeidae) appear to be the world's strongest animals. According to anecdotal reports, some species are able to support 850 times their own body mass (Matthews, 1992). If the energetic cost of carrying a gram of additional load is the

same as that of carrying a gram of body mass, such feats would involve extremely high rates of energy consumption (more than 1000 times resting metabolic rate).

I began these experiments to determine the magnitude of the loads that rhinoceros beetles can carry and to measure the metabolic energy required for carrying such loads. I hypothesized that the beetles would have very high metabolic rates in proportion to the load, e.g. when they carry a load equal to 30 times body mass, metabolic rate would increase by 30-fold compared with walking without a load.

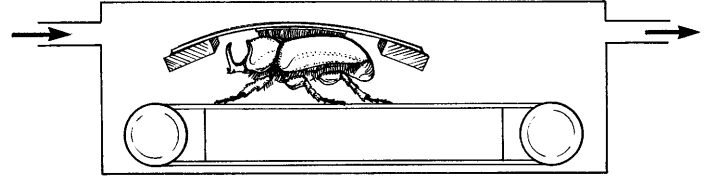
Materials and methods

Beetles (*Xylorctes thestalus*) were obtained from Hatari Invertebrates, Portal, AZ 85632, USA. To load the animal, I first glued a small piece of hook-and-loop fastener (Velcro) to its back. Then, I glued another piece of Velcro to a flexible strip of lead and glued additional weights to the ends of this strip. This allowed the loads to be changed quickly and without trauma. The weights extended in front of and behind the beetle (Fig. 1). This allowed the center of mass to be maintained near its location in the unladen animal and allowed the animal to walk without toppling. I found that the animals could move with a load of about 100 times body mass, but they would not sustain any steady speed. With loads up to 30 times body mass the beetles could walk steadily and for a long time.

I measured the rate of oxygen consumption of eight beetles as they walked slowly (1 cm s^{-1}) on a small motorized

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Fig. 1. Rhinoceros beetles (*Xylorctes thestalus*) walked on a small motorized treadmill surrounded by open-flow respirometer chamber (Herreid *et al.* 1981). Loads (lead weights) were attached so as to balance the load as symmetrically as possible.



treadmill using open-flow respirometry (Herreid *et al.* 1981) (Fig. 1). Average body mass was 2.38 g and the chamber was at room temperature, 24 °C. Rates of oxygen consumption were measured for four conditions: no additional load, and with loads equal to 10, 20 and 30 times body mass. To measure the rate of oxygen consumption, air was drawn at 77 ml s⁻¹ from a large, air-filled plastic bag through the chamber, through scrubbing tubes containing Drierite to remove water vapor and Ascarite to remove carbon dioxide, and then through an Ametek S3A/II oxygen analyzer. The rate of oxygen consumption was calculated from the product of flow rate and the difference in the fraction of oxygen between the inflow and outflow air. Values were corrected to STP. The respirometer chamber volume was approximately 170 ml. I verified that the chamber did not leak by surrounding it with various gas mixtures and monitoring that the oxygen analyzer reading was unaffected. Rates of energy consumption were calculated assuming 20.1 J ml⁻¹ O₂. I rejected trials in which the beetle pushed against the front or back of the chamber.

Results

These beetles carried additional loads remarkably cheaply (Table 1). For example, the absolute rate of energy consumption only doubled when a load equal to 10 times body mass was carried. In other words, the metabolic cost of moving a gram of additional load was more than five times cheaper than that of moving a gram of body mass (Table 1, 0.29 *versus* 1.66 W kg⁻¹). The rate of energy consumption increased linearly with additional load, but with a slope about 10 times lower than the direct proportionality expected (Fig. 2).

I was able to obtain reliable measurements of resting metabolic rate for a subset of these beetles (*N*=4). Resting

metabolism was obtained by placing the animal in the treadmill respirometer chamber which was covered with a dark cloth. Chamber temperature was 24 °C, as in the load-carrying experiments. The metabolic rates during walking for the unloaded beetles and for beetles loaded with 10, 20 and 30 times body mass were approximately 4, 8, 13 and 16 times the mean resting metabolic rate (0.41±0.07 W kg⁻¹, S.E.M.). These are all below the aerobic scope of approximately 22 predicted

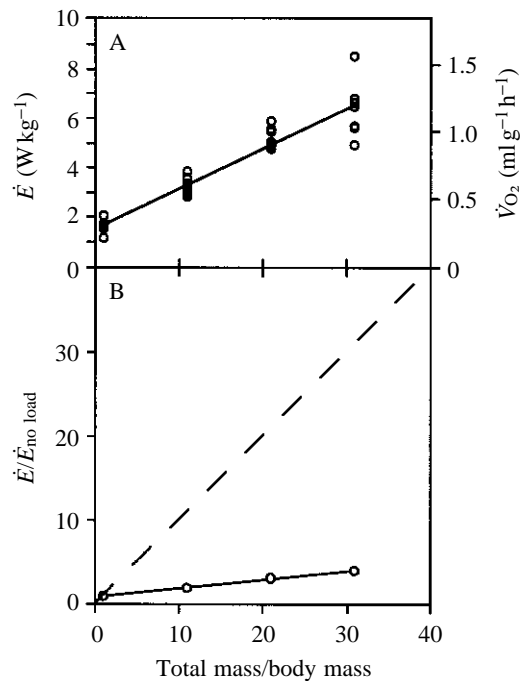


Fig. 2. (A) Rate of energy consumption (\dot{E}) increased linearly with increased load. Each open circle represents one individual (*N*=8). The least-squares linear regression equation (solid line) was: $\dot{E}=1.53+0.16M$ ($r^2=0.90$, $P=0.0001$), where \dot{E} is in W kg⁻¹ and *M* is the total mass divided by body mass. (B) Loads were carried over 10 times more cheaply than expected. The dashed line at 45° indicates the null hypothesis: that the rate of energy consumption would increase in direct proportion to the total mass. Data for many other animals including horses, humans, dogs and rats all fall along this line (Taylor *et al.* 1980). The horizontal axis is the ratio of total mass to body mass. The vertical axis is the ratio of the rate of energy consumption (\dot{E}) for each loading condition to the rate of energy consumption during unloaded walking at the same speed ($\dot{E}_{no\ load}$). The lower line is the least-squares regression for the data. Open circles indicate mean values for eight beetles. Standard error bars are within the symbols. Regression equation: $\dot{E}/\dot{E}_{no\ load}=0.91+0.098M$ ($r^2>0.99$, $P=0.0001$).

Table 1. Rates of energy consumption of rhinoceros beetles under normal and loaded conditions

Total mass/body mass	Rate of energy consumption per unit body mass (W kg ⁻¹)	Ratio of rate of energy consumption loaded/unloaded	Rate of energy consumption per unit total mass (W kg ⁻¹)
1	1.66±0.11	1.00	1.66±0.11
11	3.24±0.11	1.95	0.29±0.01
21	5.15±0.17	3.10	0.25±0.01
31	6.48±0.39	3.90	0.21±0.01

Values are mean ± S.E.M. (*N*=8).

Total mass is load mass plus body mass.

for beetles of this size (Bartholomew and Casey, 1977). The animals obviously had substantial aerobic reserves when unloaded and when carrying loads of 10 and 20 times body mass. It also seems very likely that anaerobic metabolism did not make any substantial contribution to the total rate of energy consumption when the animals were loaded with 30 times body mass because they could sustain this effort for more than 30 min.

The rate of energy consumption for these beetles when they walked unloaded ($1.66 \pm 0.11 \text{ W kg}^{-1}$) was very close to values reported for other similarly sized beetle species (Lighton, 1985; Full *et al.* 1990).

Discussion

What possible mechanisms would allow such economical load carrying? If the overall metabolic cost of locomotion is dominated by the cost of generating muscular force to support the weight of the body, then reducing the muscle force required to support a unit of load could result in more economical load carrying. For example, a more upright limb posture reduces the moment about the joints produced by the ground reaction force. A smaller joint moment requires a smaller muscle force (Biewener, 1989). Dissection did not reveal any analogous structure in these beetles. Another way to reduce the cost of generating force is to use passive structures to exert some of the joint moment. A familiar example of such structures are the ligaments which prevent extension at the wrist joints of dogs and other mammals (Alexander, 1974). However, an inspection of video recordings did not reveal any dramatic changes in limb posture when these beetles carried loads.

Another possible explanation for the economical load carrying reported here is that, when loaded with heavy weights, the beetles dragged their abdomens. Hermit crabs use this strategy and can transport their adopted shells more economically by dragging than by carrying (Herreid and Full, 1986). However, video recordings of these rhinoceros beetles walking with loads indicate that they did not use this tactic.

Economical load carriage by women of certain African tribes may be of interest in this context (Maloiy *et al.* 1986; Jones, 1989; Charteris *et al.* 1989). These people prefer to carry loads on their heads and can carry up to 20% of their unloaded body mass in this manner with no increase in metabolic rate. Recently, Heglund *et al.* (1995) have shown that at least part of the explanation for this inexpensive load carrying is a more complete exchange between the kinetic and gravitational potential energy levels of the body. This exchange is analogous to an inverted pendulum. Because the beetles in the present study walked so slowly, there is virtually no opportunity for conserving mechanical energy using an inverted pendulum mechanism. A 2 g beetle walking forward at 1 cm s^{-1} has only 10^{-7} J of kinetic energy. If all of that energy were transferred into gravitational potential energy, it would lift the beetle by only $5 \mu\text{m}$. It is clear from an inspection of video recordings that these beetles walk with at least 200 times greater vertical excursions of the center of mass (i.e. at least 1 mm).

At least two other species of insects also exhibit some degree of reduced-cost load carriage, although it is far less pronounced. Cockroaches can carry a load equal to body mass with only a 50% increase in metabolic rate above that for walking without a load (Full *et al.* 1984). Several studies have found that ants are not exceptionally economical at carrying loads (Nielsen *et al.* 1982; Lighton *et al.* 1987; Bartholomew *et al.* 1988). However, two subsequent studies report that some species of ants can carry a load equal to body mass with only about a 60% increase in metabolic rate (Nielsen and Baroni-Urbani, 1990; Lighton *et al.* 1993). Because rhinoceros beetles exhibit this economy to such an extreme, they may be the ideal animal for further investigations into the mechanism behind the more general phenomenon.

Although the mechanism which allows economical load carrying by rhinoceros beetles is not obvious, the ability to generate high forces cheaply corresponds to their lifestyle. Rhinoceros beetles are not known to carry substantial loads in their natural habitat, but they do burrow through rotting wood debris, as do many other beetle species (Evans and Forsythe, 1984). Horned beetles also exert high forces during battles for mates and thus there may have been natural selection for the ability to generate large forces economically (Otte and Stayman, 1979).

In conclusion, the mechanism that allows economical load carrying by rhinoceros beetles is not apparent. This phenomenon cannot be explained by conventional models that link biomechanics and the metabolic energy cost of locomotion.

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