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ScienceDirect
Journal of Human Evolution 54 (2008) 675–683

The energetic costs of load-carrying and the evolution of bipedalism

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Received 14 December 2006; accepted 1 October 2007

Abstract

The evolution of habitual bipedalism is still a fundamental yet unsolved question for paleoanthropologists, and carrying is popular as an explanation for both the early adoption of upright walking and as a positive selection pressure once a terrestrial lifestyle had been adopted. However, to support or reject any hypothesis that suggests carrying efficiency was an important selective pressure, we need quantitative data on the costs of different forms of carrying behavior, especially infant-carrying since reduction in the grasping capabilities of the foot would have prevented infants from clinging on for long durations. In this study, we tested the hypothesis that the mode of load carriage influences the energetic cost of locomotion. Oxygen consumption was measured in seven female participants walking at a constant speed while carrying four different 10-kg loads (a weighted vest, 5-kg dumbbells carried in each hand, a mannequin infant carried on one hip, and a 10-kg dumbbell carried in a single hand). Oxygen consumption was also measured during unloaded standing and unloaded walking. The results show that the weighted vest requires the least amount of energy of the four types of carrying and that, for this condition, humans are as efficient as mammals in general. The balanced load was carried with approximately the predicted energy cost. However, the asymmetrical conditions were considerably less efficient, indicating that, unless infant-carrying was the adaptive response to a strong environmental selection pressure, this behavior is unlikely to have been the precursor to the evolution of bipedalism.

Keywords: Bipedalism; Energetic cost; Evolution; Load carrying; Locomotion

Introduction

Bipedalism is the earliest and perhaps the most influential structural and behavioral adaptation in early hominin development, yet the origins of the evolutionary transition to bipedality are poorly understood. Regardless of whether hominin bipedalism evolved out of suspensory, quadrupedal, or terrestrial knuckle-walking locomotion (Leonard and Robertson, 2001), it is unclear whether bipedalism confers sufficient biomechanical advantages to justify its selection on the grounds of energetics alone (Richmond et al., 2001; Steudel-Numbers, 2001), which strongly suggests that other factors played key roles. Many hypotheses have been proposed to explain the selective pressures that led to the adoption of habitual bipedalism, including various foraging strategies, tool-use, thermoregulation, and predator avoidance, among others. In several of these hypotheses, the freeing up of the forelimbs for use in carrying is an important part of the explanation (Hewes, 1961; Videan and McGrew, 2002). Certainly early hominins would have needed to actively carry their dependent infants following a reduction in prehensile capacity in the hominin foot, which would have prevented infants from clinging for long durations in the way that infant apes and monkeys necessarily do in order to be transported safely. Fossil evidence from *Australopithecus afarensis* (Alemseged et al., 2006) shows that, when compared to chimpanzees, some characteristics of foot morphology are more similar to modern humans,

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doi:10.1016/j.jhevol.2007.10.004

indicating less grasping capability. The transport of food and/or tools may also have been an important factor in the evolution of bipedalism, either as part of the initial selective impetus or as an exaptive behavior (Gould and Lewontin, 1979; Videan and McGrew, 2002) that emerged after bipedalism had evolved. Provisioning of dependent females by pair-bonded males, necessitating the carrying of food items, provided the impetus for the evolution of hominin bipedalism according to a hypothesis advanced by Lovejoy (1981).

Carrying, however, bears costs as well as benefits (Ross, 2001; Schradin and Anzenberger, 2001). In order to properly evaluate any evolutionary model that uses the advantages of carrying as one of its parameters, we need quantitative data on the energetics of modern human carrying, as well as comparative data on fossil and extant hominoids. Modern human carrying has been extensively analyzed in both an ergonomic and comparative ethnographic context (Goldman and Iampietro, 1962; Soule and Goldman, 1969; Keren et al., 1981; Pierrynowsky et al., 1981; Cook and Neumann, 1987; Dziados et al., 1987; Holewijn, 1990; Bhambhani and Maikala, 2000; Wall-Scheffler et al., 2007), but there are surprisingly few comprehensive, quantitative data on the comparative costs of simple carrying tasks and, in particular, the energetic costs of infant-carrying (Wall-Scheffler et al., 2007). This information is essential for testing evolutionary hypotheses about early hominin ranging and foraging behaviors and can be used to verify predictive models of hominin locomotion (Nagano et al., 2005; Sellers et al., 2005). The energetic cost of African women performing household activities while carrying a young child on their backs has been measured. Although it has been observed that this has no obvious effect on energy expenditure (Lawrence et al., 1985), carrying has not been the focus of the experiments, and its influence has not been statistically tested. A study that compared the energetic costs of carrying a model infant in the arms compared to the costs of carrying the model in a sling found that the costs were greatly reduced by the use of a sling (Wall-Scheffler et al., 2007). This suggests that the high energetic costs of carrying an infant in the arms would have rapidly led to the development of carrying tools following the advent of bipedalism.

Limb length has been shown to be negatively correlated with the cost of transport in a range of animals (Pontzer, 2007), including chimpanzees (Sockol et al., 2007). Studies on the scaling of body mass with metabolic rate have shown that the mass-specific cost of transport decreases with increasing body mass (Steudel-Numbers, 2003; Taylor et al., 1982). This relationship is based on body mass and does not provide useful information on the cost of carrying because, unlike the addition of an external load, an increase in body mass provides an increase in locomotor musculature. An increase in the total metabolic cost of locomotion would be expected following the addition of load in order to account for increased generation of muscle force necessary to support the increased mass. However, there is considerable disagreement about whether this is actually the case. Most studies have found that, as expected, the metabolic cost of carrying in both humans and other animals does increase with load (Taylor et al., 1980; Cymerman et al., 1981; Holewijn, 1990; Wickler et al., 2001; Griffin et al., 2003; Bastien et al., 2005a). However, others have found that load has no effect on energy costs (e.g., humans carrying 7.5% of body mass [BM] in a weighted belt [Robertson et al., 1982], 20% BM in backpacks [Abe et al., 2004], and 10% BM in weighted jackets [Cooke et al., 1991], and donkeys and ponies carrying 27% BM [Pearson et al., 1998]). Other load-carrying studies have revealed the remarkable ability of African women (Maloiy et al., 1986) and Nepalese porters (Bastien et al., 2005a) to carry up to 70% and 183% of BM, respectively, in head-supported loads with much greater economy than European control subjects. These individuals are also reported to carry loads of up to 20% of their BM without increasing their oxygen consumption. The economical exchange of kinetic and potential energy during walking in African women (Heglund et al., 1995), elastic energy storage in the tendons of the lower limb, and muscle-force enhancement resulting from increased active muscle-stretch of lower limb muscles (McGowan et al., 2006) may assist carrying, although there is no good explanation for the zero energy cost ‘‘free-ride’’ phenomenon. It should be noted that studies that show no increase in metabolic cost following the addition of load are exceptions and the majority of studies do find an increase in energy expenditure.

Most laboratory-based oxygen-consumption studies conducted on humans have used a single method of load carriage, usually backpacks (Taylor et al., 1980; Cymerman et al., 1981; Holewijn, 1990; Kirk and Schneider, 1992; Quesada et al., 2000; Abe et al., 2004; Stuempfle et al., 2004; Bastien et al., 2005b). Conflicting reports on the effect of position of the load in a backpack have found that small changes in position both do (Stuempfle et al., 2004) and do not (Bobet and Norman, 1984) influence the cost of locomotion. Increased muscle activity (but not increased energetic cost of locomotion) occurs as a result of correcting for sway when a load is placed high in a rucksack (Bobet and Norman, 1984). A similar mechanism might be used to correct perturbations in gait when carrying an asymmetric load. Where work has been done on multiple methods of load carriage, it has been found that it is generally more expensive in terms of energy cost to carry a load in the hands or arms or attached to the legs than to carry the load closely attached to the trunk (Soule and Goldman, 1969; Legg, 1985; Abe et al., 2004). Studies on the different modes of stretcher-carrying (Lind and McNicol, 1968; Knapik et al., 2000) have found that transferring the stretcher load away from the hands and bearing that load on the shoulders or on the hips reduces energetic cost. Clasping a 30-kg ammunition box to the chest with both arms was the cheapest of four carrying methods investigated in a military study (Legg, 1985), and holding the box in a single hand was the most expensive. Carriage on one shoulder led to higher energy expenditure than holding the box bimanually at waist height, suggesting that asymmetry of loading leads to a higher energetic cost than carrying the load evenly. A combined front-and-back pack, or carriage of loads around the waist, tends to incur the lowest energy cost for a given load, as this optimizes stability.

Mammals unavoidably carry additional load when pregnant or during periods of food abundance when body weight increases due to fat deposits. Such loads are balanced and closely attached to the trunk so it is expected that they are carried efficiently. Experiments on humans show that the energetic cost of steady-speed treadmill-walking does increase in pregnant women (Knuttgen and Emerson, 1974), and there is a significant increase in the energetic cost of walking during the second and third trimester of pregnancy in Gambian women performing daily activities (Lawrence et al., 1985). This increase occurs despite evidence suggesting that behavioral adaptations, particularly during the third trimester of pregnancy, result in energy savings (van Raaij et al., 1990; Heini et al., 1991; Panter-Brick, 1992).

In this study, we aimed to detect changes in the cost of locomotion resulting from large alterations in the way that a mass is carried, particularly those modes of carrying thought to have been used by early hominins. A range of items (a weighted vest, dumbbells, and a mannequin infant) were chosen as loads. Each load represented a different method of load carriage and was 10 kg (approximately 18% of the participants' mean BM). The load mass chosen corresponds to the weight of a toddler rather than an infant. Toddlers do need to be carried, and the use of 10-kg loads means that the differences in oxygen consumption are larger and easier to detect than lighter loads that would require longer experimental durations. The weighted vest was used as a method of evenly distributing the mass of the load and the dumbbells provided an excellent method of carrying a large mass in one hand. The mannequin infant was included because infant-carrying would have become an important challenge for early hominins once pedal grasping capabilities were lost. Carrying an infant is an increasingly costly behavior during the period of nutritional dependence; however, in female baboons, it is estimated to be more energetically efficient to carry offspring than to allow the inefficient infant to travel independently (Altmann and Samuels, 1992). Altmann and Samuels (1992) found that the faster a female baboon traveled, the more likely she was to carry her infant. This highlights the point that the decision to carry is not necessarily influenced by instantaneous energetics but also by the potential to enhance the mother's future reproductive success. In modern humans (and presumably other infant-carrying mammals), there is a theoretical break-even point, beyond which mothers do not carry their children. It has been argued that to maximize fitness, the cost of carrying must be less than the combined cost of the child and its mother walking independently (Kramer, 1998). This argument is based on the assumption that energetic economy is paramount and does not account for the reality that energetically unfavorable carrying will occur in situations where speed or safety are important (Altmann and Samuels, 1992). Despite the fact that infant-carrying may be one of the most expensive forms of maternal care, there is little quantitative experimental data on the energetic cost of infant-carrying models (Wall-Scheffler et al., 2007) and none available for human infants.

Methods

We measured the cost of carrying loads during speed-constant, level walking in seven physically fit females of child-bearing age. Cost of locomotion was estimated from oxygen-consumption data collected while the participants stood unloaded, walked unloaded, and walked with 10 kg of additional mass under four different carrying conditions.

Participants

All seven volunteers had a good level of physical fitness. Their ages ranged from 20 to 30 years, masses from 47.9 to 63.2 kg, and heights from 1.49 to 1.68 m. Participants wore shorts, a vest, and their own training shoes. Participants had a balanced diet and were informed to eat normally before the experiment but no food was consumed for at least 30 minutes prior to, or during, data collection. The experiments reported herein were approved by the University of Salford ethics committee.

Loads carried

The loads carried were an adjustable, weighted vest (Reebok Ironwear), a 5-kg dumbbell in each hand, a 10-kg dumbbell in a single hand, and a weighted emergency-rescue-training mannequin (Ruth Lee, Model RL10, www.ruthlee.co.uk). The weighted vest contains flexible rubber weights in small pockets distributed evenly over the front and back. The mass was further adjusted by adding strips of malleable lead to the pockets. The handheld masses were cast-iron dumbbell plates with threaded bars and collars. Handheld weights are notoriously inaccurate, so all weights were checked on a laboratory balance, and the mass of the dumbbells were made up to 5 kg and 10 kg with heavy gauge copper wire. An equal amount of wire was added to each side of the dumbbell and was held in place with tape. The 10-kg dumbbell was carried in a single hand, but participants were allowed to swap hands during the trial. They were not, however, allowed to support the mass with two hands at any time. The emergency-rescue-training mannequin is manufactured with approximately realistic mass distribution and size; its mass was made up to 10-kg by hanging a small dumbbell plate around the neck with wire. This hung down the back and was held close to the torso with tape. Further wire was evenly distributed around the top of the legs and held in place with tape. The mannequin wore an all-in-one suit over the added mass, which ensured it was comfortable to carry. The mannequin was carried on the hip selected by the participant (Fig. 1) and remained on the same hip for the duration of data collection. Although there is no direct evidence to suggest that early hominins carried infants asymmetrically, carrying infants astride the hip is common in many modern cultures. The hip provides a natural "shelf" and the position is thought to provide social and sensory benefits for the infant (Jelliffe, 1975). All the load conditions were $10\,kg \pm 1\%$ after

Fig. 1. Participant walking on treadmill wearing Metamax unit and carrying mannequin.

adjustment. The average mass carried was about 18% of the participants' mean BM.

Measurements

Each walking task was carried out on a treadmill (Vison T9250, Wisconsin, US) at a constant speed (3.7 km h^{-1}, 1.028 m s^{-1}) chosen as the speed at which the net cost of human walking is minimum (Sellers et al., 2005). Throughout the experiments, the participants wore a face mask and breath-by-breath oxygen consumption (VO_2) was logged directly via a telemetered oxygen analyzer (Metamax, Cortex, Germany). The apparatus was calibrated according to manufacturer's instructions. The major advantage of this equipment over more traditional Douglas bags is that it facilitates longer data-collection intervals, which considerably reduces measurement error. A lightweight neoprene harness was worn by the participants and the portable oxygen-analyzer unit was passed around the back of the neck and attached to the harness with Velcro. The total weight of the apparatus was less than 1 kg and has previously been shown to have a negligible effect on energy costs (Coen et al., 1999; Meyer et al., 2003). The order of carrying conditions was randomized, and participants were given a minimum of 5 minutes to become accustomed to wearing the mask and walking on the treadmill. Data collection commenced after this period of acclimation and continued for 10 minutes for each condition. Participants rested for a minimum of 5 minutes between tasks. Data for analysis were taken after the first 2 minutes and from before the final minute of data collection. These are fairly arduous experimental conditions, taking approximately 90 minutes per participant with a total walking distance in excess of 3 km while carrying awkward 10-kg loads. Only data where the respiratory-exchange ratios were <1.0 were included, indicating that energy was supplied primarily by oxidative metabolism.

Oxygen consumption was converted to standard temperature and pressure automatically by the Metamax system, and energy was calculated using the standard factor of 20.1 kJ per liter of O_2 (Schmidt-Nielsen, 1983). Cost of locomotion (J s^{-1}) was calculated by dividing the total energy expenditure by the measurement time for each condition. Cost of transport (J kg^{-1} m^{-1}) was calculated by dividing the mass-specific cost of locomotion by the treadmill velocity. Net values were calculated by subtracting the value for unloaded standing.

Results

Oxygen consumption increased with the addition of all loads. Table 1 shows the mass of each participant and the experimental results for each participant in terms of the gross-mass-specific cost of locomotion for all the experimental conditions. The mean gross and net cost of locomotion for all the conditions are shown in Fig. 2.

Table 1
Participant mass (kg) and mass-specific gross cost of locomotion for each carrying condition (J s^{-1} kg^{-1})

Participant	Participant mass (kg)	Unloaded standing (J s^{-1} kg^{-1})	Unloaded walking (J s^{-1} kg^{-1})	Vest (J s^{-1} kg^{-1})	Mass in each hand (J s^{-1} kg^{-1})	Mannequin (J s^{-1} kg^{-1})	Mass in one hand (J s^{-1} kg^{-1})
1	60.7	1.39	3.36	3.75	4.34	4.83	4.50
2	57.2	1.40	3.09	3.57	4.03	4.52	4.45
3	47.9	1.24	3.61	4.18	4.26	4.72	5.57
4	51.3	1.22	3.53	4.03	4.14	4.80	4.69
5	50.3	1.54	3.94	3.83	–	5.46	4.32
6	63.2	1.39	4.08	4.50	4.77	–	5.48
7	61	1.37	4.08	4.53	4.97	5.71	–
Mean	55.1	1.36	3.67	4.06	4.42	5.01	4.83
SE	2.3	0.04	0.14	0.14	0.14	0.18	0.21

A dash indicates that data are unavailable due to respiratory-exchange ratios >1.

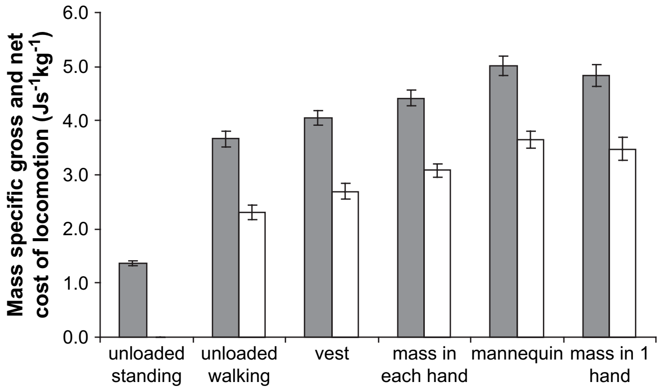

Fig. 2. Mean mass-specific gross (solid bars) and net (hollow bars) cost of locomotion ($J\ s^{-1}$) ± SE for each condition.

A one-way ANOVA with repeated measures was carried out on all data, excluding unloaded standing and unloaded walking, and showed a significant effect of the type of load carried on the gross-mass-specific cost of locomotion ($F_{(3,9)} = 12.217$, $p = 0.002$). Five paired *t*-tests determined the significance of the differences between the conditions. There was a significant effect on gross cost of locomotion between standing unloaded and unloaded walking ($t = 16.542$, df = 6, $p < 0.0005$), between unloaded walking and walking with the 10-kg vest ($t = 4.512$, df = 6, $p = 0.003$), between walking with the 10-kg vest and walking with a 5-kg mass in each hand ($t = 3.876$, df = 5, $p = 0.012$), and between walking with a 5-kg mass in each hand and walking with the 10-kg mannequin ($t = 10.211$, df = 4, $p = 0.001$). There was no significant difference in gross-mass-specific cost of locomotion between carrying the 10-kg mannequin and carrying a 10-kg mass in one hand ($t = 0.503$, df = 4, $p = 0.641$). Conversion to net cost of locomotion (Fig. 2) has no effect on the statistical analysis; all the conditions were significantly different except for the mannequin and the mass in one hand.

Figure 3 shows the data transformed to show the gross and net cost of transport for all of the experimental conditions. Since this is just a linear transformation, there is no effect on the statistical analysis.

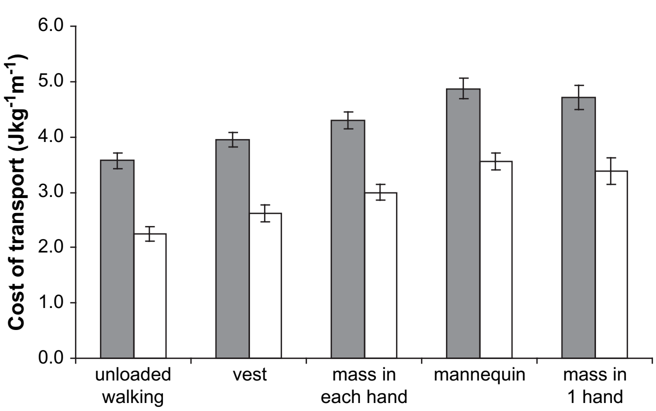

Fig. 3. Mean gross (solid bars) and net (hollow bars) cost of transport ($J\ kg^{-1}\ m^{-1}$) ± SE.

Discussion

Measurement of oxygen consumption during different carrying tasks has given us a valuable insight into the economy of different methods of carrying a 10-kg mass. Oxygen consumption increased with the addition of load, and the method of load carriage had considerable influence on energy expenditure, as shown by the range of energetic costs found when the loads were carried in different positions. The evenly distributed mass in the weighted vest required the least energy expenditure. Balanced dumbbell weights in each hand were significantly more expensive to carry than the weighted vest. The energetic costs of carrying the mannequin on one hip and the dumbbell in a single hand were not significantly different from each other but were both significantly more expensive than any of the other methods of carrying.

To put our results in the context of general mammalian energetics, we compared our results to those of other load-carrying studies in humans (Soule and Goldman, 1969; Quesada et al., 2000; Griffin et al., 2003; Bastien et al., 2005a) and in large quadrupeds (Lawrence and Stibbards, 1990). We plotted the ratio of net loaded to net unloaded metabolic rate against the ratio of loaded (body mass plus load) to unloaded (body mass only), following the format used by Marsh et al. (2006) (Fig. 4). In the case of Nepalese porters (Bastien et al., 2005a), metabolic and mass data were not available, so the net metabolic ratio and mass ratio were taken from Marsh et al. (2006). Where net metabolic data were not available (Quesada et al., 2000), an estimated resting metabolic rate of 1.5 W/kg (Marsh et al., 2006) was used to calculate net values. The metabolic ratios during walking and during running with relatively light loads are similar. Taylor et al. (1980) compared the metabolic costs of loaded running and found that, at a constant speed, VO_2 increased in direct proportion to load in horses, dogs, rats, and humans carrying between 7 and 27% of BM.

Our bimanual-dumbbell data and weighted-vest data correspond well with other mammalian load-carrying studies at mass ratios of about 1.2 (approximately 20% BM) (Fig. 4). In these studies, the mass is carried symmetrically, and the net metabolic ratio is greater than the mass ratio. However, the data from the mannequin and the 10-kg mass in one hand indicate a marked reduction in carrying economy. The high metabolic-to-mass ratio found with carrying the mannequin on one hip and the 10-kg mass in one hand is exceeded only when loads are carried on the feet. Nepalese porters who use a head strap to support loads in a basket are very economical carriers (Bastien et al., 2005a) (Fig. 4). Training to carry head-supported loads starts in early childhood (Panter-Brick, 1992) and seems essential for the economical carriage seen in Nepalese porters and African women. Loads carried on the head in a weighted helmet by untrained people (Soule and Goldman, 1969) were carried with an average metabolic-to-mass ratio that was less economical than that of experienced head-carriers. Previous studies have shown that untrained people can only manage loads of up to 15% of BM supported by the head (Maloiy et al., 1986). Learning to minimize movement of the center of mass may be key to

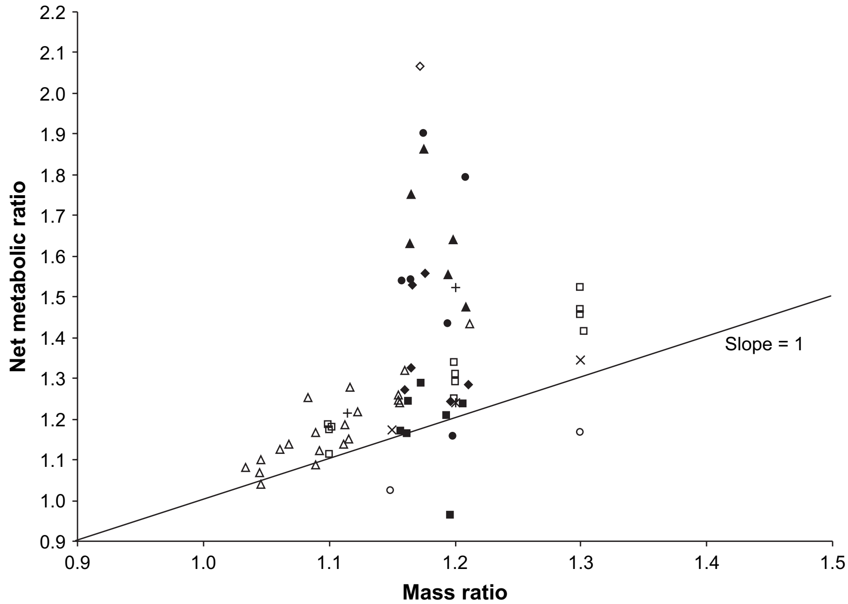

Fig. 4. Metabolic response to load-carrying in walking mammals. The ratio of net loaded to net unloaded metabolic rate as a function of the ratio of loaded to unloaded body mass. The line with a slope of 1.0 is included for reference. Symbols are as follows: △ = large quadrupeds (Lawrence and Stibbards, 1990); □ = human data for loads carried in a waist strap (Griffin et al., 2003); + = human data for a load carried in each hand (Soule and Goldman, 1969); * = untrained human carrying a head load; ◇ = human carrying loads on the feet (Soule and Goldman, 1969); ○ = Nepalese porters carrying head loads (Bastien et al., 2005a); × = human data for loads carried in backpacks (Quesada et al., 2000); ■ = data from this study for loaded vests; ◆ = data from this study for a load carried in each hand; ▲ = data from this study for carrying a mannequin on one hip; ● = data from this study for carrying a load in a single hand.

reducing the cost of locomotion when carrying head-supported loads (Soule and Goldman, 1969; Maloiy et al., 1986). By far, the most expensive method of carrying loads is on the feet (Soule and Goldman, 1969). It should be noted however that the foot loads were made by filling double-walled boots with mercury. This method of loading impaired flexion and extension of the ankle joint during walking, which could in itself have contributed to the increased energetic cost.

There is variation in the energetic cost of carrying both within and between species and the data shown here are intended only as representative examples. One notable example of within-species variation in carrying efficiency is the negative relationship between female human pelvis width and energetic cost of infant-carrying (Wall-Scheffler et al., 2007).

As in most carrying studies, we found no evidence of the ‘‘free-ride’’ phenomenon, as all our loads led to a marked increase in oxygen consumption compared to unloaded walking. The phenomenon is rarely seen with loads greater than about 10% BM in untrained carriers. We suspect that only highly trained carriers can carry significant loads with no increase in energetic cost, and even then, only when the load is carried symmetrically. Whether the ability to carry moderate weights for no energetic cost was important in the evolution of human bipedalism is an interesting question but will require a better understanding of the biomechanics of this phenomenon before we can begin to address it.

In addition, when interpreting the results of metabolic studies it is important to consider the validity of the assumptions behind indirect calorimetry. Indirect calorimetry enables metabolic rate to be calculated from the rate of oxygen consumption. The amount of food intake by participants affects the accuracy of the energy calculation; up to 23% error has been found when participants eat less than they spend metabolically (Webb et al., 1980). The type of food and the time of food consumption prior to experimentation also influences the volume of oxygen consumed (Jequier et al., 1987) and therefore has a bearing on the calculation of metabolic rate. Few studies provide such information, which can make interpretation of results difficult.

Our experimental data show that loads in each hand and the weighted vest are carried with approximately the same economy as other symmetrical mammalian carrying. However, the specific case of a heavy asymmetric load, in particular an infant, is relatively expensive, which has considerable implications when considering optimal foraging and ranging strategies in human and early hominin groups. The high cost of infant-carrying by humans suggests that this behavior is unlikely to have been the driving force behind the evolution of bipedalism. However, regardless of the key activity preceding the evolution of habitual bipedal locomotion, carrying will have occurred as an exaptive behavior if not the principle adaptive response to an environmental selection pressure. Carrying an asymmetric load is not only energetically expensive but also a relatively complex behavior in terms of balance, indicating that this might only have occurred once bipedalism was well established. Studying long-term evolutionary changes in a single species has limitations (Garland et al., 1999) and comparisons of carrying behavior among the great apes would provide a broader, interspecific approach.

With the exception of the weighted vest, we concentrated on loads that required active transport, as it is unlikely that the earliest hominins had the technological capacity to manufacture a passive carrying device like a sling. A sling could be created from strips of animal hide or woven from plant materials, but both are difficult unless you have sharp chopping tools or stone flakes to prepare the material. We included the vest to demonstrate what we considered would be the most economical method of load carriage but consider passive carrying devices unlikely to have had a bearing on the initial evolution of bipedalism. Infants can be passively and symmetrically carried on the shoulders without the use of an external device, but this mode of carrying is not practical with a mannequin and is rarely used by females and so was not included in this study. Our results indicate that loads of up to about 20% of body weight can be carried efficiently when balanced symmetrically between the hands, and thus if carrying was an important factor in the evolution of bipedalism, then it is more likely that the objects being carried were relatively small and easily grasped (such as single items of food or raw materials) rather than larger and more unwieldy burdens that would require bimanual and/or asymmetrical transport.

Our findings have implications for models of early hominin life histories and subsistence strategies. Great ape and Old World monkey mothers carry their offspring in ventral or dorsal positions that do not compromise the mother's locomotor behavior, and by analogy with human and mammalian experimental data, these symmetrical and ''hands free'' carrying positions, in which the load is positioned close to the carrier's center of mass, are likely to be energy efficient. Furthermore, in these primates, infant-carrying is discontinued at a developmental stage when the infant's body mass is less than 20% of the mother's body mass (Hoff et al., 1983; Altmann and Samuels, 1992), and so these animals do not incur the higher energy costs that would be associated with transporting heavier loads. An ancestral bipedal hominin infant is likely to have required active rather than passive carrying due to the combination of reduction of prehensile capacity in the hominin infant foot and reduced opportunities for infant clinging due to upright maternal posture and a possible reduction in graspable maternal body hair. Active carrying, especially when the load is carried asymmetrically, is energetically expensive, and coupled with the higher transport costs associated with the characteristically short leg length of early hominins (Sockol et al., 2007), it would have resulted in early hominin infant-carrying being comparatively costly in energetic terms. Our findings imply that, in later human evolution, selection for the manufacturing of carrying aids would have been likely in order to reduce the energetic costs of transporting larger and more unwieldy objects. Indeed, experimental data indicate that the use of a sling can reduce the cost of infant-carrying by 16% (Wall-Scheffler et al., 2007).

In this study, the net metabolic rate was calculated by subtracting resting metabolic rate from the total metabolic rate (Griffin et al., 2003; Marsh et al., 2006). This does not tell us the extent to which the load affected the postural cost of standing. Previous studies have shown no increase in metabolic rate with load during standing (Maloiy et al., 1986; Marsh et al., 2006). Pandolf et al. (1977) did, however, find a small increase in the cost of standing with a 10-kg load compared to standing unloaded. Data on the energetic cost of loaded standing, although interesting, are not available and would not affect our conclusion that energy expenditure is influenced by the method of load carriage.

Energetic cost is not the only factor affecting carrying ability. Local muscle fatigue can limit load carriage, and in this study, discomfort in the arms, after carrying the 10-kg dumbbell and the mannequin, was the reason participants wanted to rest rather than physical exhaustion. The mannequin, unlike carrying a child, is a ''dead weight''; it is unable to actively hold on and does no work in maintaining posture or balance, which may make it harder to carry. However it does not wriggle and the mannequin can easily be carried in the most comfortable position for the adult. It would certainly be useful to compare these data with carrying data for children and compare different methods of carrying a child. In addition, none of our participants were experienced at carrying infants and none had the benefit of training through the gestational period. An interesting extension of this study would be to include mothers of young children in order to address whether conditioning influences the results. Studies on carrying in nonhuman primates would also provide an interesting basis for comparison to these data. Very young human infants need to be cradled to support the head, which is likely to add to the energetic cost. However, lack of head support at birth is due to the very large postnatal brain size in modern humans and may not have been a problem for less altricial primates.

Conclusions

In summary, our results show that the method of load carriage has considerable influence on energy expenditure. Evenly distributed weights, such as the weighted vest, are the most economical to carry. Balanced weights in each hand match average mammal predictions and asymmetrical weights, such as the mannequin carried on the hip and the single dumbbell, are more energetically costly than predicted and are jointly the two most metabolically expensive methods of carrying. Unless infant-carrying was the adaptive response of individuals subjected to a strong environmental selection pressure, the high energetic cost indicates that it was unlikely to have been the precursor to bipedal locomotion.

Acknowledgements

Thanks to Anmin Liu and Steve Horton for help with data collection and to The University of Salford for use of their facilities. Advice and suggestions from anonymous referees are gratefully acknowledged. This work was funded by NERC grants NE/C520447/1 and NE/C520463/1.

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