

Froude Number Corrections in Anthropological Studies

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ABSTRACT The Froude number has been widely used in anthropology to adjust for size differences when comparing gait parameters or other nonmorphological locomotor variables (such as optimal walking speed or speed at gait transitions) among humans, nonhuman primates, and fossil hominins. However, the dynamic similarity hypothesis, which is the theoretical basis for Froude number corrections, was originally developed and tested at much higher taxonomic levels, for which the ranges of variation are much greater than in the intraspecific or intrageneric comparisons typical of anthropological studies. Here we present new experimental data on optimal walking speed and the mass-specific cost of transport at that speed from 19 adult humans walking on a treadmill, and evaluate the predictive power of the dynamic similarity hypothesis in this sample. Contrary to the predictions of the dynamic

similarity hypothesis, we found that the mass-specific cost of transport at experimentally measured optimal walking speed and Froude number were not equal across individuals, but retained a significant correlation with body mass. Overall, the effect of lower limb length on optimal walking speed was weak. These results suggest that the Froude number may not be an effective way for anthropologists to correct for size differences across individuals, but more studies are needed. We suggest that researchers first determine whether geometric similarity characterizes their data before making inferences based on the dynamic similarity hypothesis, and then check the consistency of their results with and without Froude number corrections before drawing any firm conclusions. *Am J Phys Anthropol* 131:27–32, 2006. © 2006 Wiley-Liss, Inc.

Comparisons of locomotor variables between populations or taxa of different sizes are always problematic. One must assess how much of any observed difference is due to different adaptations, and how much is simply due to size. For example, if a difference in energetic efficiency for walking at a given speed is found between biomechanical models of a human and AL 288-1 (“Lucy,” *Australopithecus afarensis*), is this difference due to a less efficient form of bipedalism in AL 288-1, or simply because AL 288-1 was modeled to walk at a speed that was too fast for her short stature?

The Froude number has been used widely as a way to adjust for size differences when making comparisons of gait parameters or other nonmorphological locomotor variables such as energetic efficiency. While the Froude number is usually used to compare taxa at high taxonomic levels (e.g., Alexander, 1976; Alexander and Jayes, 1983) or over large size ranges (Griffin et al., 2004a), the dynamic similarity hypothesis (which is the theoretical basis for Froude number corrections) has also been applied to intraspecific or intrageneric comparisons of interest to anthropologists, such as human adults and children (e.g., Alexander, 1984; DeJaeger et al., 2001), different human populations (e.g., Minetti et al., 1994, 2000; Saibene and Minetti, 2003), fossil hominins (e.g., Alexander, 1984; Kramer, 1999; Kramer and Eck, 2000; Saibene and Minetti, 2003; Wang et al., 2004), and nonhuman primates (e.g., Vilensky et al., 1988; Pontzer and Wrangham, 2004; Raichlen, 2004). In most anthropological applications, the Froude number is used to calculate an “equivalent” speed for each group at which measures of energetic efficiency or other nonmorphological parameters can be compared.

The Froude number was originally developed as a dimensionless variable that could be used to estimate, from tests on small-scale models, the power needed to

propel full-scale ships against the resistance of their bow waves (McMahon and Bonner, 1983; Alexander, 1991; Vaughan and O’Malley, 2005). It was applied to the locomotion of animals moving on the water surface (e.g., Prange and Schmidt-Nielsen, 1970), but Alexander (1984, 1991) and Alexander and Jayes (1983) first introduced the Froude number to terrestrial systems by suggesting that the motion of two animals of different sizes will be dynamically similar (such as both trotting or both walking) if they are moving at equal Froude numbers. More precisely, two animals moving in a dynamically similar manner will have equal ratios of all lengths, times, and forces. Because velocity is simply distance (a length) per unit time, two animals moving in a dynamically similar manner should also have equal ratios of their velocities. In this way, many quantities of one animal can be related to those of the other animal. The dynamic similarity hypothesis was proposed (Alexander and Jayes, 1983; Alexander, 1991) as an extension of geometric similarity (isometry) to predict the scaling of nonmorphological variables. A basic assumption of the dynamic similarity hypothesis is that the underlying morphology is geometrically similar, because without

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geometric similarity, the length criterion that is necessary for dynamic similarity is violated.

The Froude number (v^2/gl) is proportional to the ratio of kinetic energy ($mv^2/2$) to potential energy (gml), which are related to inertia and gravity, respectively (Duncan, 1953; Alexander, 1991), where v is velocity, g is the acceleration due to gravity, m is body mass, and l is a "characteristic length," usually limb length. An application of the Froude number to terrestrial systems is plausible because many workers believe that exchanges between kinetic and potential energy are important in minimizing the energetic cost of locomotion, particularly for bipedal walking (Cavagna et al., 1977; Willems et al., 1995). Among other expectations, the dynamic similarity hypothesis of Alexander and Jayes (1983) and Alexander (1984) predicts that the minimum mass-specific cost of transport (the amount of energy required to move a unit weight over a unit distance) for different animals will be equal and occur at the same Froude number. This was given as an important reason why animals tend to move in a dynamically similar manner (Alexander and Jayes, 1983; Alexander, 1984).

Limb length is thought to be a particularly appropriate "characteristic length" to be used to calculate the Froude number, because limb length strongly influences the pendular aspects of an animal's gait. The "inverted pendulum" model suggests that the energetic cost of walking is minimized by exchanges between the kinetic energy of the body moving forward and the potential energy produced by the vertical rise of the center of mass. Extensive experimental evidence supports this model (e.g., Cavagna et al., 1977; Willems et al., 1995; Griffin et al., 2004b). The individual limbs also function, to some extent, in a pendular manner, particularly during walking (Mochon and McMahon, 1980; Myers and Steudel, 1997). In running, the fluctuations of kinetic and potential energy during a stride tend to be in phase (Cavagna et al., 1977; Willems et al., 1995), and energetic savings are thought to accrue through the storage and recovery of elastic strain energy.

A number of studies comparing taxa at high taxonomic levels (e.g., Alexander and Jayes, 1983) or over large size ranges (e.g., Griffin et al., 2004a) showed a good fit between observed gait parameters and the predictions of the dynamic similarity hypothesis. Consequently, the Froude number is becoming a commonly used method for assessing equivalencies in the gait of animals differing in size in terrestrial locomotor systems, among humans, nonhuman primates, and fossil hominins (e.g., Alexander, 1984; Vilensky et al., 1988; Minetti et al., 1994, 2000; Kramer, 1999; Kramer and Eck, 2000; DeJaeger et al., 2001; Saibene and Minetti, 2003; Pontzer and Wrangham, 2004; Raichlen, 2004; Wang et al., 2004). A potential problem with applications within anthropology is that, while limb length tends to scale isometrically at high taxonomic levels (e.g., Steudel and Beattie, 1993), this may not be the case at lower taxonomic levels. Isometric scaling may occur for any particular study at a low taxonomic level, but the vast majority of articles applying this approach in an anthropological context (e.g., Alexander, 1984; Minetti et al., 2000; DeJaeger et al., 2001; Saibene and Minetti, 2003; Pontzer and Wrangham, 2004; Raichlen, 2004) do not present any data indicating whether or not their subjects show geometric similarity in their morphological elements. Thus, they may be applying the dynamic similarity model in situations where an important underlying assumption (geometric similarity) is not met.

Further, Donelan and Kram (1997, 2000) questioned the utility of the dynamic similarity hypothesis as a predictor of gait parameters in humans. They artificially altered the level of gravity to which subjects were exposed by having them walk or run while their body weight was variably supported by a bicycle seat attached to springs. Variation in many, though not all, of their gait parameters did not follow the predictions of the dynamic similarity hypothesis. One might argue that their results were compromised because their method of reducing gravity did not alter the gravitational forces experienced by the limbs. However, if exchanges between the potential and kinetic energy of the center of mass, rather than of the limb itself, are the major source of energetic savings in human walking, as many workers believe (Cavagna et al., 1977; Willems et al., 1995), this element of their experimental design should not be a problem.

The present study is an attempt to evaluate the utility of Froude number corrections for anthropological studies (or other studies at low taxonomic levels) by testing two specific expectations of the dynamic similarity hypothesis. We evaluate: 1) whether the speed at which walking is most economical (i.e., the mass-specific cost of transport is lowest) in adult humans occurs at the same Froude number; and 2) whether cost is indeed equal across individuals at this speed (Alexander and Jayes, 1983; Alexander, 1984; Donelan and Kram, 1997).

MATERIALS AND METHODS

We collected data on 19 adult human subjects who had about a 19% difference in lower limb length between the two most extreme subjects. This difference is actually greater than the difference between the "pygmy" and European means (about 18%) in Minetti et al. (1994). To directly determine optimal walking speed and the energetic cost of transport at optimal walking speed for individuals, the subjects walked on a motor-driven treadmill at four different walking speeds, 1.16, 1.25, 1.34, and 1.43 msec^{-1} , all near previously reported speeds for energetic optimality (Booyens and Keatinge, 1957; Bhambhani and Singh, 1985). Their expired gases were monitored using a SensorMedics Vmax 29c automated respiratory gas analysis system, which gives breath-by-breath analysis and printouts of oxygen consumed and carbon dioxide produced. The system was calibrated for flow rate and accuracy of gas analysis before every trial. The subjects walked for 12 min at each speed. Cost for each speed was determined by averaging the rate of oxygen consumption (VO_2) over a 4-min period, beginning after the subject had walked for at least 6 min. At least three separate trials for each subject at each speed were averaged for each individual. Two subjects showed identical minimum costs at two different walking speeds. For these subjects, both minima were included in the data for analysis. We also measured each subject's height, weight, and lower limb length. Lower limb length was measured as two separate variables, femur length and tibia length, which were subsequently summed. Femur length was measured from the greater trochanter to the knee midpoint. Tibia length was measured from the knee midpoint to the lateral malleolus of the fibula. These were summed to represent total lower limb length. While this method excludes the height of the foot, it has proved to be a useful measure of lower limb length (Steudel-Numbers and Tilkens, 2004). In human walking, this method closely reflects the functional length of the lower

TABLE 1. Subject number, lower limb length, mass, optimal walking speed, and cost of transport at optimal speed for all 19 subjects included in analyses

Subject number	Optimal walking speed (msec ⁻¹)	Lower limb length (cm)	Mass (kg)	Cost of transport at optimal walking speed (ml O ₂ m ⁻¹ kg ⁻¹)
1	1.34	72.30	64.70	0.164
3	1.25	85.55	95.02	0.161
8	1.34	78.30	52.03	0.128
9	1.16	76.10	81.44	0.154
10	1.43	77.30	55.65	0.141
13	1.34	78.30	63.34	0.141
20	1.43	83.05	76.92	0.171
22	1.34	84.95	56.56	0.133
23	1.43	85.80	71.94	0.130
24	1.34	77.10	59.27	0.118
26	1.34	82.10	57.01	0.144
26	1.43	82.10	57.01	0.144
30	1.34	81.80	72.17	0.146
31	1.34	80.00	61.53	0.154
32	1.16	79.10	57.01	0.149
32	1.34	79.10	57.01	0.149
33	1.16	78.90	91.85	0.177
34	1.25	80.55	70.58	0.181
35	1.16	71.40	76.92	0.195
36	1.34	79.45	83.71	0.175
38	1.34	86.30	77.37	0.176

limb, unlike in small mammals, where a crouched posture is adopted when walking, so that anatomical and functional length can be very different. Subjects lower limbs length, mass, optimal walking speed, and cost of transport at that speed are given in Table 1.

The cost per unit time of walking increases curvilinearly with speed (Cotes and Meade, 1960; Menier and Pugh, 1968; Falls and Humphrey, 1976). When cost is calculated per unit distance rather than per unit time (the cost of transport), there is a speed (or speeds) at which cost is at a minimum. Locomotion at this speed (or speeds) is less costly per unit distance than at other speeds. The dynamic similarity hypothesis predicts, “Different animals moving in dynamically similar fashion have equal costs of transport” (Alexander and Jayes, 1983). These authors were speaking about mass-specific costs of transport. Thus, it follows from this statement that 1) animals walking at the speed at which they have their minimum mass-specific costs of transport should be walking at the same Froude number; and 2) their mass-specific costs should be equal at this speed (see also Donelan and Kram, 1997).

To determine whether cost at optimal walking speed is indeed the same across individuals, we calculated the correlation between the mass-specific cost of transport at the experimentally measured optimal speed for each individual and their mass (kg). If costs were equal, the relationship should be nonsignificant. Further, we tested to see whether the Froude numbers at optimal walking speed were indeed equal across subjects. To do this, we calculated the correlation between Froude number and mass. If Froude numbers were the same, the relationship should be nonsignificant.

While many workers are very careful in interpreting “l” in the formula for Froude number simply as “characteristic length” as in the original model of Alexander and Jayes (1983) and Alexander (1984), lower limb length is becoming the standard measurement (Kramer, 1999; Kramer and Eck, 2000; Minetti et al., 2000; DeJaeger et al., 2001). This seems appropriate because lower limb length is, after all, the length of the limb as a pendulum,

and approximates the height of the center of mass under the inverted pendulum model. We wondered whether the Froude number calculated from limb length was preferable to calculating the Froude number in some other way, such as body mass^{1/3}, particularly because the geometric similarity of lower limb length is not always present. Consequently, we calculated the Froude number in two ways: one, as given above, Froude(LL), using lower limb length as the “characteristic length,” and the other, Froude(MASS^{1/3}), by substituting the cube root of mass for limb length in the equation above.

RESULTS

We tested the prediction of the dynamic similarity hypothesis that “different animals moving in dynamically similar fashion have equal costs of transport” (Alexander and Jayes, 1983). It follows from this statement that different animals should have minimum costs of transport that are equal, which should occur while walking at the same Froude number, to satisfy dynamic similarity (see also Donelan and Kram, 1997). Contrary to the predictions of the dynamic similarity model, the cost of transport (ml O₂ m⁻¹ kg⁻¹) at the optimal walking speed was not constant, but retained a substantial correlation with body mass ($r = 0.643$, $P = 0.002$; Fig. 1). We also tested the prediction that individuals walking at their optimal walking speed should be moving at the same Froude number. The correlation of Froude(LL) at optimal speed with mass, which should be insignificant according to the prediction, was in fact significant ($r = 0.509$, $P = 0.018$; Fig. 2). The correlation of Froude(MASS^{1/3}) with mass was also significant ($r = 0.684$, $P = 0.001$; Fig. 3). Overall, the effect of lower limb length on optimal walking speed was weak ($r = 0.383$, $r^2 = 0.147$, $P = 0.087$; Fig. 4).

DISCUSSION

The results of our study suggest that the Froude number may not be an effective way for anthropologists to

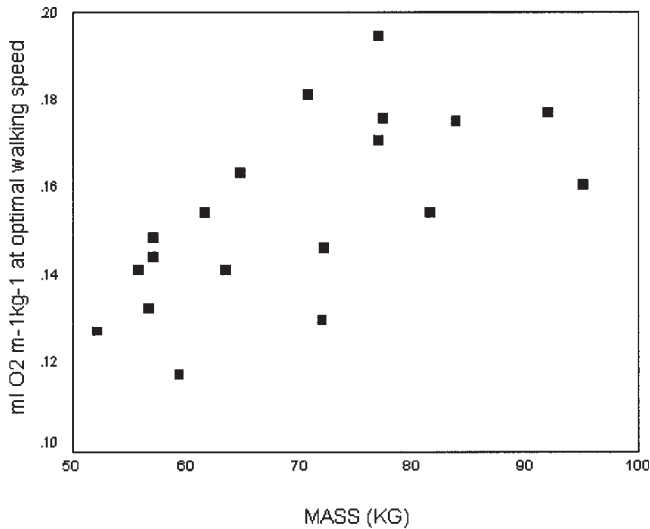


Fig. 1. Mass-specific cost of transport at optimal walking speed is significantly correlated with mass ($r = 0.643$, $P = 0.002$).

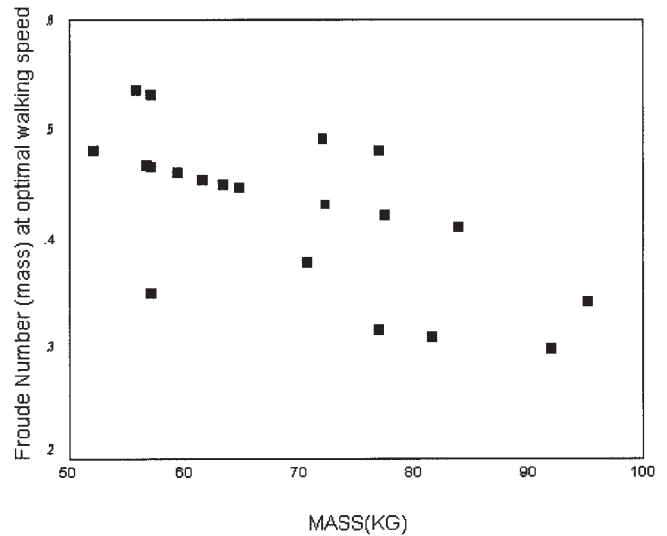


Fig. 3. Froude number calculated using cube root of mass as “characteristic length” at optimal walking speed retains substantial correlation with mass ($r = 0.684$, $P = 0.001$).

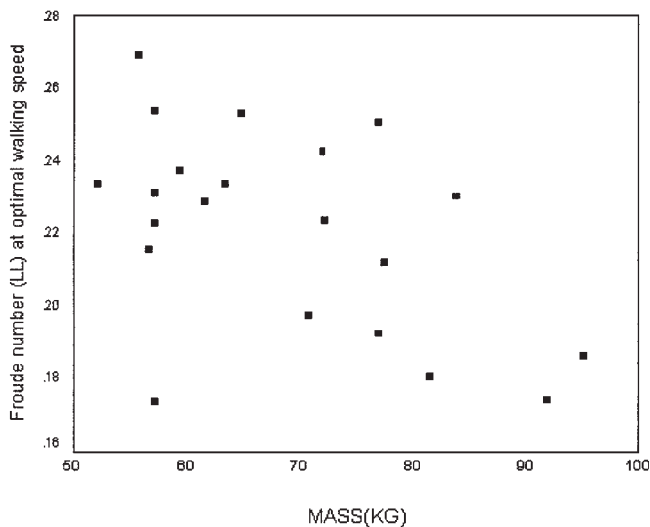


Fig. 2. Froude number calculated using lower limb length as “characteristic length” at optimal walking speed retains a substantial correlation with mass ($r = 0.509$, $P = 0.018$).

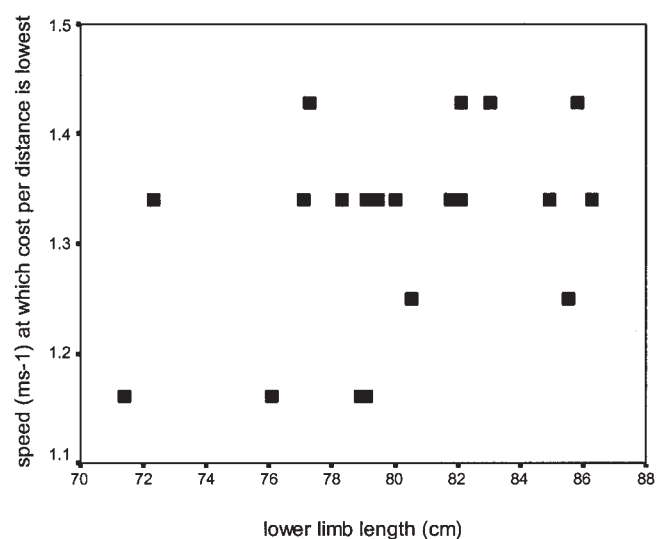


Fig. 4. Relationship between speed at which cost per meter (ml O₂/m) is minimum, and lower limb length (cm) ($r = 0.383$, $P = 0.087$).

adjust for size differences, but more studies are needed (see also Steudel-Numbers and Tilkens, 2004). Why are these results so different from studies that showed congruence between Froude number and locomotor variables (e.g., Alexander and Jayes, 1983; Griffin et al., 2004a)? As indicated above, dynamic similarity is an extension of geometric similarity. To have dynamic similarity, there must first be geometric similarity (Alexander and Jayes, 1983; Alexander, 1991). Therefore, one possible reason for our results is that the subjects were not geometrically similar. Limb length, in fact, was not significantly correlated with mass ($r = 0.138$, $r^2 = 0.019$, $P = 0.55$; Fig. 5). In studies across higher taxonomic levels or larger size ranges, different animals may also not be geometrically similar, but they may be geometrically similar enough relative to the magnitude of

the size differences and range of speeds (Steudel and Beattie, 1993). In support of this explanation, in a study of horses over a larger range of body sizes, in contrast to our results, Griffin et al. (2004a) found a strong correlation between limb length and mass ($r = 0.99$). In the present study, deviations from geometric similarity are probably much larger relative to the differences in sizes of subjects and range of speeds, and thus may be large enough to compromise the dynamic similarity hypothesis. Naturally, when variation in a trait is small, a given level of error variance becomes a greater proportion of the total variance. As indicated above, the vast majority of studies applying the dynamic similarity model in an anthropological context did not report whether their sample showed geometric similarity (Alexander, 1984; Minetti et al., 2000; DeJaeger et al., 2001; Saibene and

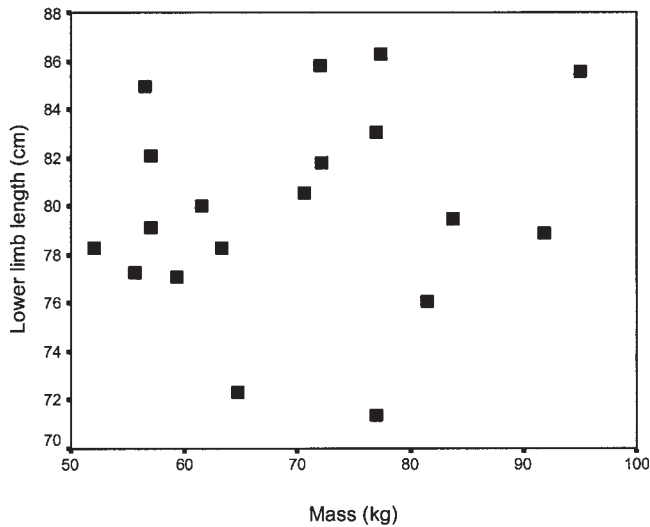


Fig. 5. Relationship between limb length and body mass was not significant in our sample ($r = 0.138$, $r^2 = 0.019$, $P = 0.55$).

Minetti, 2003; Pontzer and Wrangham, 2004; Raichlen, 2004). It may be that the dynamic similarity hypothesis only makes sense when applied across samples showing greater variation in size and speeds.

The results were very similar using Froude(LL) and Froude(MASS^{1/3}). The fact that Froude(LL) and Froude(MASS^{1/3}) had similar relationships with mass suggests that lower limb length has no particular value in calculating the Froude number over other measures of “characteristic length,” such as the cube root of mass. It is interesting that the predictions of the dynamic similarity model under two different methods of calculating “characteristic length” produced such similar results.

This discussion of geometric similarity leads to another point about using the Froude number to scale for differences in size when there are also differences in geometry. If two individuals of different sizes who are also geometrically dissimilar are compared and have different mass-specific costs of transport at the same Froude number, this does not necessarily imply that one individual is more economical than the other. What this could imply is that the dynamic similarity hypothesis failed in this situation (was rejected), because one of the predictions of the hypothesis is that the mass-specific costs of transport should be equal for individuals walking at the same Froude number. Because dynamic similarity assumes geometric similarity, it can be extremely circular to use Froude number scaling when looking for differences in gait parameters between individuals of different sizes who are also geometrically dissimilar.

When humans, nonhuman primates, or fossil hominins of different sizes are compared for gait parameters or other nonmorphological locomotor variables, some method must be found to correct for size differences. Many studies used the regression residual of a variable regressed against mass as a size-independent value (e.g., Garland and Janis, 1993; Steudel and Beattie, 1995). The elements of the Froude number (limb length and travel velocity) are both quite highly correlated with body mass (Garland, 1983; Steudel and Beattie, 1993). The possibility exists, therefore, that the Froude number works simply as a surrogate for mass. Future work should include data acquisition of gait variables over a

wider range of sizes and speeds than included in this study, to allow comprehensive evaluation of the merits of the Froude number. For the moment, we suggest that before drawing conclusions, researchers should check the consistency of their results with and without Froude number corrections. Furthermore, investigators need to establish whether geometric similarity is present in their data before applying the dynamic similarity model.

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