



The evolution of human running: Effects of changes in lower-limb length on locomotor economy

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Received 19 September 2006; accepted 9 April 2007

Abstract

Previous studies have differed in expectations about whether long limbs should increase or decrease the energetic cost of locomotion. It has recently been shown that relatively longer lower limbs (relative to body mass) reduce the energetic cost of human walking. Here we report on whether a relationship exists between limb length and cost for human running. Subjects whose measured lower-limb lengths were relatively long or short for their mass (as judged by deviations from predicted values based on a regression of lower-limb length on body mass) were selected. Eighteen human subjects rested in a seated position and ran on a treadmill at 2.68 m s^{-1} while their expired gases were collected and analyzed; stride length was determined from videotapes. We found significant negative relationships between relative lower-limb length and two measures of cost. The partial correlation between net cost of transport and lower-limb length controlling for body mass was $r = -0.69$ ($p = 0.002$). The partial correlation between the gross cost of locomotion at 2.68 m s^{-1} and lower-limb length controlling for body mass was $r = -0.61$ ($p = 0.009$). Thus, subjects with relatively longer lower limbs tend to have lower locomotor costs than those with relatively shorter lower limbs, similar to the results found for human walking. Contrary to general expectation, a linear relationship between stride length and lower-limb length was not found.

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Keywords: Limb length; Energetics; Human running

Introduction

Lower-limb length is known to vary substantially across hominin lineages. Some examples are the short lower-limb lengths of *Australopithecus* as compared to later *Homo* and the short lower limbs of Neandertals as compared to contemporaneous populations of anatomically modern humans. Paleanthropologists have generally hypothesized that shorter lower limbs would have resulted in reduced economy in the cost of transport (Trinkaus, 1981; Jungers, 1982; Jungers and Stern, 1983; Holliday and Falsetti, 1995; Steudel and Beattie, 1995), though the possibility of increased economy has also

been proposed (Kramer, 1999; Kramer and Eck, 2000). The biomechanical arguments behind both expectations are very reasonable. Those supposing that longer limbs should reduce cost argue that longer limbs result in longer stride length, which in turn should result in fewer strides for a given distance, and hence greater economy. Those supposing that longer limbs should increase cost argue that a longer limb has a greater moment of inertia, which would require more input of energy to overcome, and hence increasing cost.

The relevance of the role of lower-limb length in running is especially trenchant in light of Bramble and Lieberman's (2004) recent suggestion that selection for endurance running (ER), in particular, may have been a key selective basis for the change in broad elements of morphology, including limb length, from *Australopithecus* to *Homo erectus* (see also Carrier, 1984). Might the longer lower limbs of *Homo* be a result of selection for increased economy in ER? Steudel-Numbers and Tilkens (2004) showed that longer lower limbs reduce the energetic cost of

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human walking. Does the same effect obtain in human running? Ferretti et al. (1991) found that the cost of walking ($\text{ml O}_2 \text{ kg}^{-1} \text{ km}^{-1}$) was similar in African pygmies and Europeans, while the cost of running was lower in pygmies. In contrast, Minetti et al. (2004) reported that the cost of walking was significantly higher in pygmies, while the cost of running was not significantly different between pygmies and Europeans for within-speed comparisons. Neither group of authors made an attempt to evaluate the significance of limb length specifically. Because pygmies differ from Europeans in a variety of ways in addition to shorter limb lengths (on average)—including shorter stature, lower total body mass, and likely in numerous other variables such as body fat—their results are difficult to use to assess the ER hypothesis. Given the importance suggested specifically for ER in human evolution (Carrier, 1984; Bramble and Lieberman, 2004), it seems worthwhile to more carefully evaluate the effect of differences in lower-limb length on the cost of human running. Here we test (1) whether the relationship between lower-limb length and the cost of running is qualitatively or quantitatively different than that for human walking and (2) whether correlated changes in stride length, the most widely expected explanation for such a phenomenon among paleoanthropologists (see above), is involved.

Methods

All subjects were carefully notified about the purpose of the study and possible risks, and they signed a consent form approved by the University of Wisconsin IRB. Subjects whose measured lower-limb lengths were long or short relative to body mass, as judged by deviations from predicted values (based on the regression of lower-limb length on mass from the morphometrics in Steudel-Numbers and Tilkens, 2004) were selected. Lower-limb length was measured as the sum of two separate variables—thigh length and shank length. Thigh length was measured from the greater trochanter to the midpoint of the knee. Shank length was measured from the midpoint of the knee to the lateral malleolus of the fibula. Only subjects whose body-mass index (BMI) was less than 25.0—normal according to McArdle et al. (2001)—were included.

We measured rates of oxygen consumption and carbon dioxide production in eighteen human subjects between 18 and 30 years of age while they sat comfortably resting or ran on a treadmill at 2.68 m s^{-1} on six separate occasions using a SensorMedics Vmax 29c automated respiratory-gas analysis system, which gives breath-by-breath analysis of expired gases. Before every trial, the system was calibrated for (1) flow rate by testing known flow rates and (2) accuracy of gas analysis by testing known gases. All subjects exercised regularly and had no difficulty maintaining the pace. Measurement of resting metabolic rate always preceded the running trial. We chose 2.68 m s^{-1} (=6.0 mph) as a relatively modest jogging speed that is comfortably above reported preferred walk-run transition speeds (Thorstensson and Roberthson, 1987; Hreljac, 1995) but that could be readily maintained aerobically for the 12 min required for our data collection. Subjects with absolutely longer limbs tend to

transition from a walk to a run at higher speeds than do shorter-limbed subjects (Hreljac, 1995), and thus those individuals in our study who had absolutely longer limbs in addition to longer limbs in relation to their body mass were running closer to their walk-run transition speed; this situation may have put them at a slight disadvantage, and we would expect the longer-limbed individuals to have slightly higher costs as a result. The subjects ran for 12 min and their rates of oxygen consumption (VO_2) over the last four minutes were averaged to estimate VO_2 for that trial. The final VO_2 value for each subject was the average value of the three most similar values from separate trials to minimize normal daily metabolic variation.

We also collected data on stride length for all but two of our subjects (the schedules of the latter individuals did not allow time for a final laboratory session). For the collection of data on stride length, subjects ran without the VO_2 -collection mask. Stride length (complete stride length, two footfalls) was determined by timing the period it took a subject to run ten strides from “heel down” on stride zero to “heel down” on stride ten. During a single session, a subject’s stride length was measured numerous times to ensure consistency and at least three repetitions were averaged for the final value. This average was divided by ten to give the number of strides per second (stride frequency). The speed (2.68 m s^{-1}) was divided by the stride frequency to get each subject’s stride length.

The minimum cost of transport is the cost to run for a given distance minus the “postural cost”—the y-intercept of the regression of cost on velocity (e.g., Taylor et al., 1970)—and can thus be referred to as the “net cost of transport.” The total cost of transport itself actually decreases with increasing speed. This counterintuitive result stems from the fact that the total, or “gross,” cost of transport includes the “postural cost,” which is essentially the cost of maintaining general metabolism during the time interval measured. During the time spent in locomotion, the body continues the metabolic activities of other organ systems, which are included in the calculation of cost of transport (COT). Thus, if one travels faster, one arrives sooner and a smaller amount of general metabolism is included in the measurement of locomotor cost. Because “postural costs” come from many activities not involving posture, we will here refer to such cost as general metabolism (GM). The net COT, by subtracting GM, removes the speed dependency of cost, which can be seen graphically in Fig. 1 of Steudel-Numbers (2006). Average values for GM in humans are 1.36 times resting metabolic rate (FAO/WHO/UNU, 1985; DeJaeger et al., 2001). Thus, we calculated the net COT (L/km) as the cost to travel 1 km at 2.68 m s^{-1} , subtracting 1.36 times the resting metabolic rate that would occur during the time taken to travel 1 km at that speed. For comparison, we also looked at the gross COT (L/km) at 2.68 m s^{-1} .

We did not attempt to vary the locomotor tasks assigned to our subjects based on dynamic similarity (Froude number). The Froude number ($=v^2/2g$, where v is velocity, g is the acceleration due to gravity, and l is a “characteristic length”) has been suggested as a way of predicting the scaling of gait

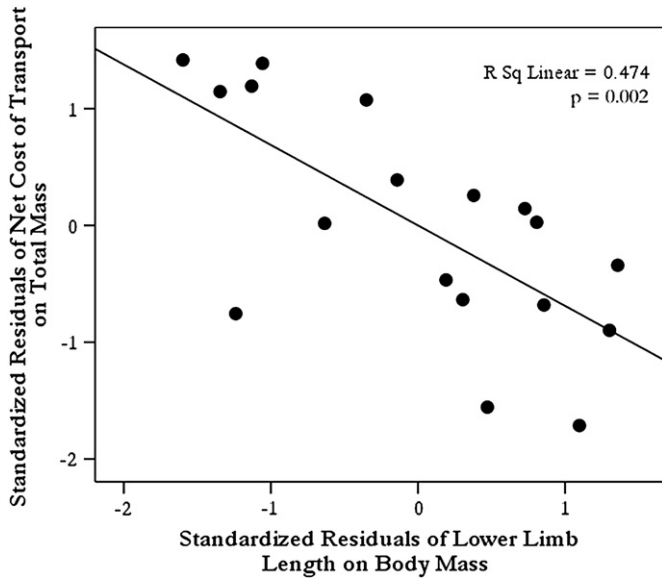


Fig. 1. The relationship between the net cost of transport and lower-limb length, controlling for body mass.

variables to lower-limb length (Alexander and Jayes, 1983; Alexander, 1984). Thus, stride length and speed are expected to be proportional to lower-limb length (Alexander and Jayes, 1983; Alexander, 1984). A number of studies, however, have shown that Froude number may not be an appropriate correction for humans. Cavanagh and colleagues (Cavanagh and Williams, 1982; Cavanagh and Kram, 1989) found only weak relationships between lower-limb length and gait variables in human running. Steudel-Numbers and colleagues (Steudel-Numbers and Tilkens, 2004; Steudel-Numbers and Weaver, 2006) have further shown that the effect of lower-limb length on optimal walking speed is weak and that Froude number is not an appropriate correction in the size range represented by adult humans.

We analyzed the cost data in two ways. In the first case, we determined the partial correlation between net COT (L/km) and lower-limb length controlling for body mass. In the second case, we determine the partial correlation between gross COT (L/km) and lower-limb length controlling for body mass. We also used regression analysis to create the standardized residuals of the regression of cost on mass and of lower-limb length on mass so that the relationship of cost and lower-limb length with the effects of body mass removed could be graphed. We did not divide each variable by body mass to create the “mass-specific cost of locomotion” reported by many authors because we prefer to avoid the many drawbacks associated with ratios (Sokal and Rohlf, 1981). Instead, we analyzed the relationship between cost, lower-limb length, and body mass more formally as individual correlated variables to more carefully document the relationship between cost and lower-limb length with the effect of body mass removed. We also determined the relationships among stride length, lower-limb length, and both measures of cost, again controlling for body mass where relevant.

Results

The morphometrics and locomotor costs of the subjects are provided in Table 1, together with stride length. The ratio of CO₂ produced to O₂ consumed was always less than one, implying aerobic respiration only.

We found significant negative relationships between relative lower-limb length and cost in both analyses. The partial correlation between net COT (L/km) and lower-limb length controlling for total mass was $r = -0.69$ ($p = 0.002$). The partial correlation between the gross COT at 2.68 m s⁻¹ (L/km) and lower-limb length with the same control was $r = -0.61$ ($p = 0.009$). Thus, subjects with relatively longer lower limbs tend to have lower locomotor costs than those with relatively shorter lower limbs, similar to the results found for human walking (Steudel-Numbers and Tilkens, 2004). Figure 1 is a graph of the standardized residuals of the net COT on mass versus the residuals of lower-limb length on mass. The similarity of these partial correlation values suggests that the results are robust with respect to differences in the manner of calculating the cost of running.

The equation relating the gross COT (L O₂ m⁻¹) to mass (kg) and lower-limb length (cm) is:

$$\text{Gross COT} = 4.76 + 0.33(\text{mass}) - 0.15(\text{lower} - \text{limb length});$$

$$r = 0.96 \quad (1)$$

surprisingly similar to the equation for walking. The constants and the coefficients for lower-limb length in walking and running are not significantly different (95% confidence intervals overlap). The coefficient for mass, however, does differ, being significantly higher in running (95% confidence intervals do

Table 1

Descriptive statistics of the subjects in the present study, including morphometrics, gait, and cost variables

Individual	Sex	Lower-limb length (m)	Mass (kg)	BMI	Stride length (m/stride)	Gross cost of transport (L/km)	Net cost of transport (L/km)
1	M	0.924	72.2	19.6	2.190	14.96	12.89
2	F	0.735	50.0	20.0	1.911	10.75	9.58
4	M	0.880	63.8	19.9	2.014	11.81	10.28
5	M	0.799	72.2	24.6	2.221	16.28	14.73
6	M	0.791	73.1	24.5	2.119	16.72	15.27
7	M	0.792	69.9	23.8	—	13.34	11.86
8	M	0.937	79.9	21.4	—	17.27	15.10
9	M	0.899	69.5	21.7	2.005	12.90	10.56
11	F	0.840	63.6	21.6	2.014	11.24	9.42
12	F	0.852	62.2	21.2	1.947	11.97	10.19
13	M	0.865	82.8	24.3	2.264	19.91	17.46
14	F	0.751	60.6	23.7	1.913	13.37	12.16
15	F	0.830	59.1	20.9	1.915	11.93	10.50
16	F	0.853	65.7	22.5	1.990	12.43	11.04
18	M	0.990	96.4	23.8	2.230	20.34	18.25
19	F	0.750	51.1	20.0	1.908	10.46	8.99
20	M	0.783	62.3	22.0	1.941	12.56	11.07
21	M	0.950	90.5	24.6	1.867	19.77	17.80

not overlap). The equation relating the net COT ($L O_2 m^{-1}$) to mass (kg) and lower-limb length (cm) was:

$$\text{Net COT} = 6.11 + 0.319(\text{mass}) - 0.18(\text{lower - limb length});$$

$$r = 0.96 \quad (2)$$

For both gross COT and net COT, the models that include lower-limb length have higher coefficients of correlation than those models that use body mass alone ($r = 0.94$ for gross; $r = 0.92$ for net). This result indicates a significant impact of lower-limb length on metabolic cost and economy, especially for net COT costs.

The relationships between body mass and cost, lower-limb length, and stride length can be seen in Fig. 2. All relationships are significant. Stride length, however, does not have a significant linear relationship with lower-limb length (Fig. 3) with or without the effect of mass removed by residual analysis ($r = 0.35$, $p = 0.184$ with mass; $r = 0.23$, $p = 0.42$ without mass). Thus, it does not appear that changes in stride length account for the proportion of energetic cost accounted for by the increase in lower-limb length reported here.

Discussion

These data demonstrate that, when body mass is controlled, increased lower-limb length results in a lower cost of running, whether expressed as the net cost of transport or as the gross cost of transport. This result confirms the theoretical expectation of many workers (Jungers, 1982; Jungers and Stern, 1983; Carrier, 1984; Steudel and Beattie, 1995; Bramble and Lieberman, 2004; Pontzer, 2005). This result differs, however, from previous experimental results looking at the effect of limb length on the energetic cost of running (Pontzer, 2005). While the expectations of the LiMb model described by Pontzer (2005) predict the inverse relationship between limb length and locomotor cost reported here, Pontzer's (2005) data do not show this pattern. Pontzer (2005), describing data from nine human subjects at four walking speeds and three running speeds, found that locomotor cost "was negatively correlated with limb length only at moderately fast walking speeds" (p. 1522). Here, we demonstrate a negative relationship between cost and limb length in human running. One possible explanation for the difference in our results may be that speed was not held constant when testing the LiMb model, while in the data presented here, speed was held constant. If the subjects in Pontzer's (2005) study tended to select different running speeds, this would make direct comparison of their locomotor costs problematic.

The fact that relatively longer lower limbs decrease the cost of locomotion, coupled with the relatively rapid increase in lower-limb length observed with the appearance of *Homo* (particularly *H. erectus*) after a long period of relative stasis in lower-limb length in *Australopithecus* (Ward, 2002), corroborates the widespread view that daily movement distances increased sharply quite early in the evolution of *Homo*. That a decrease in cost with longer lower limbs characterizes human running and human walking is consistent with the

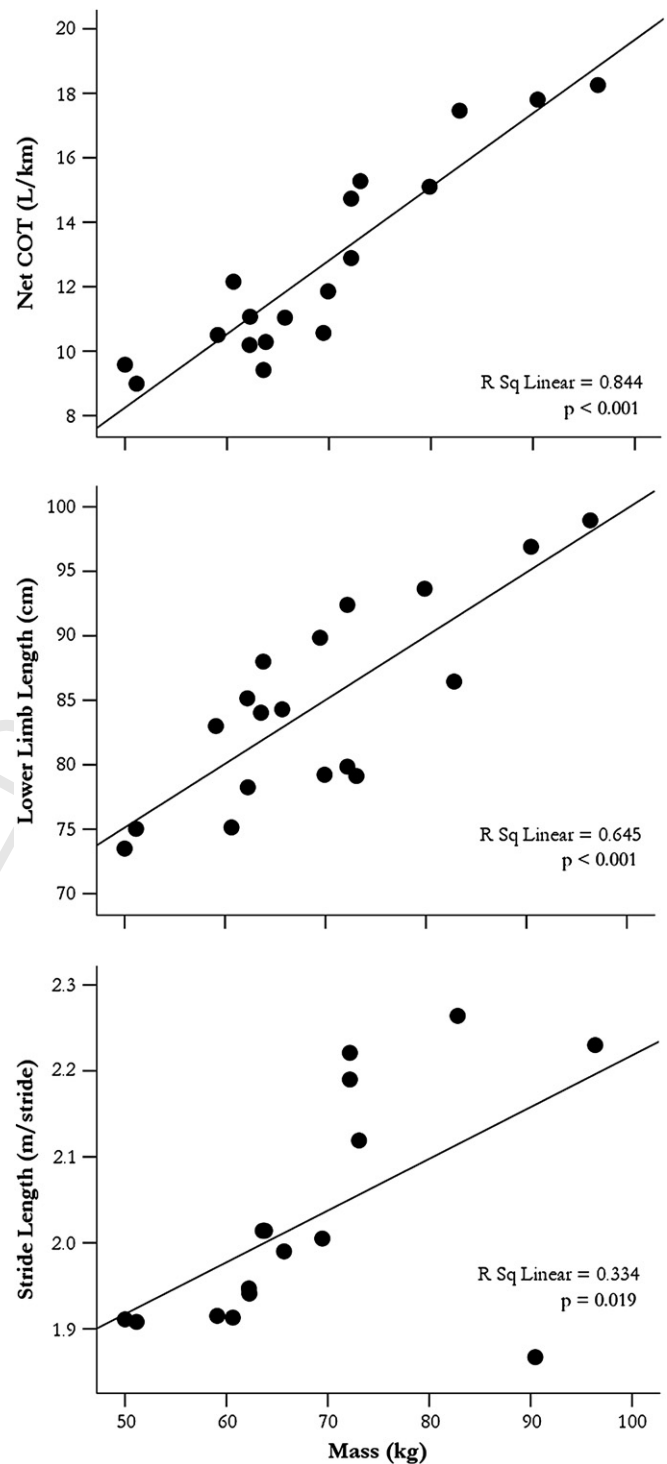


Fig. 2. The relationships between body mass and cost, lower-limb length, and stride length.

arguments of Carrier (1984) and Bramble and Lieberman (2004) that selection for effective endurance running may have been important in determining the postcranial morphology observed in *Homo*. *Homo erectus* would have been a much more economical runner than *Australopithecus*. Do these results allow us to further evaluate whether selection for walking versus running was important in the evolution of

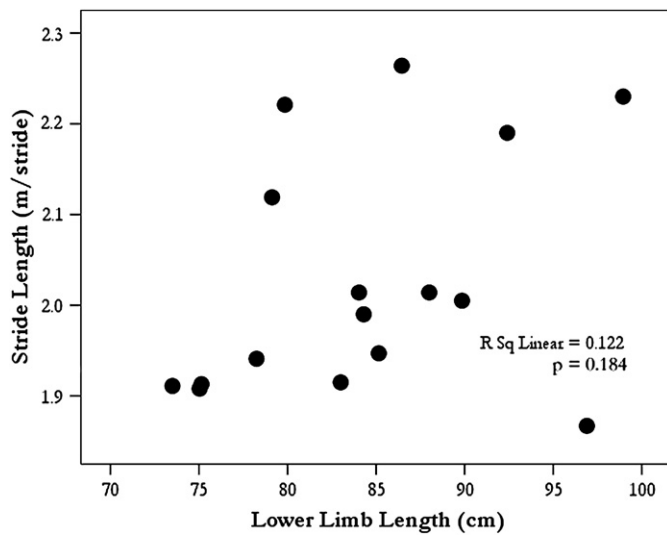


Fig. 3. The linear relationship between lower-limb length and stride length.

Homo? Unfortunately, we think not. A comparison of the present results with those for human walking (Steudel-Numbers and Tilkens, 2004) shows that relative lower-limb length has similar effects on the economy of both walking and running, although the effect is slightly larger in walking than in running. Based on Eq. (1) presented above and that given in Steudel-Numbers and Tilkens (2004), a 70-kg human would see a decrease of approximately 10% in their gross cost of transport in going from a 75 cm to an 85 cm lower-limb length in running. The same morphological change would decrease the gross cost of walking by approximately 16%. Given the similarity in the locomotor morphologies of *H. erectus* and modern humans, it seems likely that members of the former taxon used both gaits. Any increase in locomotor efficiency produced by longer lower limbs in walking would have been approximately matched by increased efficiency in running, making it impossible to evaluate which gait was the primary target of selection for locomotor efficiency.

The fact that aspects of locomotor morphology may be useful in both walking and running is true for the vast majority of variables cited by Bramble and Lieberman (2004) as adaptations for endurance running; for example, the wide shoulders and narrow waists seen in *Homo* may benefit counter-rotation of the trunk (Witte et al., 1991) relative to the hips in both gaits in order to minimize total motion of the center of mass. Nonetheless, additional work may reveal elements of morphology/physiology that confer particular advantage in one or the other gait (Lieberman et al., 2006).

Short-legged *Homo* species, such as the Neandertals, would thus have run and walked less efficiently than contemporaneous populations of anatomically modern humans. Hence, previous assessments (Steudel-Numbers and Tilkens, 2004; Weaver and Steudel-Numbers, 2005) of the substantial caloric consequences of the relatively shorter lower limbs on walking are probably accurate independent of the gait used. The short lower limbs of *Australopithecus* also would have led to inefficient locomotion on the ground. The fact that short lower

limbs, nonetheless, persisted for millions of years (Ward, 2002) suggests one of two possibilities. One is that there was countervailing selection for short limbs because of some other locomotor activity, such as more efficient climbing (Steudel-Numbers and Tilkens, 2004). A second possibility is that the daily movement distances on the ground for *Australopithecus* were quite small, similar to those observed in extant woodland chimpanzees. If this was the case, the costs of terrestrial locomotion would have been a relatively small part of the total daily energy budget of these animals, resulting in low levels of selection for efficiency in that activity.

The usual expectation among anthropologists about the effects of lower-limb length on cost has been that longer lower limbs should result in lower costs because it takes fewer strides to travel a given distance (Schmidt-Nielsen, 1984; Fancy and White, 1987; Janis and Wilhelm, 1993; Steudel and Beattie, 1995; Bramble and Lieberman, 2004). Empirically, this can be shown to be true in interspecific comparisons (Heglund and Taylor, 1988), but not in running humans (Cavanagh and Williams, 1982; Cavanagh and Kram, 1989; present study). Thus, further investigation should be undertaken of the mechanisms driving the relationship between lower-limb length and cost.

Conclusions

We have shown that relatively longer lower limbs result in more efficient running, similar to previous work on human walking and consistent with the expectation of many paleoanthropologists. We also show that the explanation for this result is not that longer-limbed individuals take longer strides, as is widely supposed. Because longer lower limbs decrease locomotor cost to a similar extent in human walking and running, these results do not allow us to evaluate whether selection for efficiency in walking or running may have led to the elongation of the limbs of *Homo*. Further work should be done to explore the mechanical reasons why longer limbs result in greater locomotor efficiency.

Acknowledgements

The L.S.B. Leakey Foundation provided financial support for this project. The authors thank Marcella Myers for useful insights and the anonymous reviewers for helpful comments on the manuscript. We also thank Mike Tilkens for assistance with data collection and our many subjects for cheerfully donating so much of their time.

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