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Short Communications

The relative limb size of *Homo naledi*

Sarah Traynor [a, *], David J. Green [b, d], John Hawks [c, d]

[a] Academic Affairs, School of Medicine and Public Health, UW-Madison, Madison WI, 53706, USA
[b] Department of Anatomy, School of Osteopathic Medicine, Campbell University, Buies Creek, NC, 27506, USA
[c] Department of Anthropology, UW-Madison, Madison, WI, 53706, USA
[d] Evolutionary Studies Institute and Centre for Excellence in Palaeosciences, University of the Witwatersrand, Private Bag 3, Wits 2050, South Africa

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1. Introduction

Observational and experimental research from extant nonhuman primates and modern humans can be applied to the study of early hominin variation and adaptation in body form. Limb proportions—including limb length, joint size, and limb robusticity—can provide information about arboreal behavioral activity (Stern and Susman, 1983; Susman et al., 1984), bipedal efficiency (Steudel-Numbers and Tilkens, 2004; Steudel-Numbers et al., 2007; Hora et al., 2014), thermoregulation (Wheeler, 1984; Ruff, 1991, 1993, 1994; Tilkens et al., 2007; Holliday and Hilton, 2010; Wall-Scheffler, 2014), and phylogenetic relationships (Holliday, 1997, 1999, 2012; McHenry and Berger, 1998a,b; Richmond et al., 2002; Green et al., 2007; Prabhat et al., 2021).

Selection pressures acting on limb proportions played an important role in the mosaic transition from *Australopithecus* to *Homo*. Most hominin taxa fall between extant apes and modern humans (*Homo sapiens*) with regard to limb length and limb size proportions (Aiello and Dean, 1990; Richmond et al., 2002; Haeusler and McHenry, 2004; Holliday, 2012; Heaton et al., 2019; Prabhat et al., 2021). *Australopithecus* and early *Homo* taxa possessed more apelike, forelimb-dominant proportions relative to the more humanlike, hindlimb-dominant proportions of later *Homo*. The taxa with more humanlike proportions are generally thought to have a reduced arboreal repertoire and an increased reliance on bipedal locomotion (McHenry and Berger, 1998a, b; Haeusler and McHenry, 2004; Green et al., 2007; Prabhat et al., 2021). However, most extinct hominins are thought to have incorporated both arboreal and terrestrial components into their positional behaviors (Susman et al., 1984; McHenry and Berger, 1998a,b; Haeusler and McHenry, 2004; Green et al., 2007; Heaton et al., 2019; Gordon et al., 2020).

The earliest members of the genus *Homo*, such as *Homo habilis* and *Homo floresiensis*, demonstrate limb proportions that are dissimilar to modern humans, suggesting a more mosaic transition in 'bauplan' from *Australopithecus* to *Homo* (Haeusler and McHenry, 2004; Holliday, 2012). Wood and Collard (1999) argued for reassigning *H. habilis* to the genus *Australopithecus*, citing the australopith-like limb proportions, among other skeletal evidence. Regrettably, the postcranial material attributed to *H. habilis* is highly fragmentary and less certain in attribution, so the limb estimates remain uncertain (Richmond et al., 2002). Because of its retention of many primitive apelike and australopith-like postcranial and cranial features, even though *H. floresiensis* is geologically much younger, this species is thought to have separated early from the common ancestors of other members of the genus *Homo*, with its lineage originating near the branching point at which the *H. habilis* lineage began (Morwood and Jungers, 2009; Dembo et al., 2015).

Significant limb proportion variation occurs among individuals attributed to *Homo erectus* individuals as well. For example, the earlier *H. erectus* Dmanisi individual, D4507, exhibits humerofemoral indices that are significantly different from those of a large sample of Pleistocene and Holocene *H. sapiens*. In contrast, these indices for KNM-WT 15000 are similar to those of *H. sapiens* (Holliday, 2012). To further blur the distinction between early *Homo* and *Australopithecus*, *Australopithecus afarensis* and *Australopithecus sediba* more closely approximate a humanlike pattern of upper to lower limb joint size proportions (McHenry and Berger, 1998a; Green et al., 2007; Haile-Selassie et al., 2010; Holliday et al., 2018) though both species demonstrate the typical *Australopithecus* interlimb length proportion that falls between those of

* Corresponding author.
E-mail address: setraynor@wisc.edu (S. Traynor).

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Pan troglodytes and *H. sapiens* (Holliday et al., 2018; Heaton et al., 2019). This overlap among different representatives of *Homo* and *Australopithecus* suggests that limb proportions did not set all branches of the genus *Homo* apart from other hominins.

An evaluation of the limb proportions of *Homo naledi* is critical for understanding the transition from *Australopithecus* to *Homo*. Many aspects of *H. naledi* morphology suggest that it is phylogenetically rooted deep in the genus *Homo* (Dembo et al., 2016; Hawks and Berger, 2016; Berger et al., 2017; Argue et al., 2017). Although present at ~300 ka (Dirks et al., 2017), *H. naledi* demonstrates many traits similar to *A. afarensis* or *Australopithecus africanus* (e.g., small cranial capacity, scapular and pelvic morphology, phalangeal curvature). Accordingly, a secure estimate of relative upper to lower limb size in *H. naledi* would shed more light on variation in the genus *Homo* and help us evaluate the range of locomotor strategies present in the common ancestor of *H. erectus* and other anatomically primitive forms of *Homo*.

The overall Dinaledi Chamber sample of *H. naledi* includes elements from at least 15 individuals. To date, few of these have been matched to the same skeleton (Berger et al., 2015), although this work continues (Bolter et al., 2020). The Lesedi Chamber sample consists of at least three individuals, including a partial adult skeleton (LES 1; Hawks et al., 2017). Garvin and colleagues (Garvin et al., 2017) estimated the maximum length of the most complete adult *H. naledi* humerus and tibia from the Dinaledi Chamber to derive a humerotibial length index. Given the possibility that these bones belong to different individuals, they compared this value to resampled distributions of humerotibial length indices from *P. troglodytes*, *Gorilla* spp., and single population of smaller-bodied Kulubnarti individuals from medieval Nubia. The *H. naledi* value fell within the 95% confidence interval of the Kulubnarti human distribution and well below the *Pan* and *Gorilla* distributions, suggesting that *H. naledi* had a humanlike relative limb length (Garvin et al., 2017). Lower limb length may be very informative about the adaptation of *H. naledi* to striding bipedalism (Garvin et al., 2017; Marchi et al., 2017; Walker et al., 2019), with additional evidence provided by its derived foot morphology (Harcourt-Smith et al., 2015). However, the relative joint sizes and shaft robusticity of *H. naledi* are also informative with regard to this adaptation. In addition, although some features of the hands and shoulders provide evidence that *H. naledi* was adapted to climbing (Kivell et al., 2015; Feuerriegel et al., 2017, 2019), establishing the relative limb size of *H. naledi* with a large sample of *H. naledi* elements will provide useful context for evaluating hypotheses about the locomotor habits of this group in light of other morphological analyses. Prabhat et al. (2021) estimated the relative limb size of the LES 1 partial skeleton using four upper and lower limb elements. They determined the relative limb size of LES 1 to be humanlike as the relative limb size value of LES 1 fell within the modern human distribution and well outside of the hylobatids, *Gorilla* spp., *Pan* spp., and *Pongo* spp. distributions (Prabhat et al., 2021). Here we use a wider range of unassociated elements from the Dinaledi and Lesedi Chambers and resampling techniques to estimate the relative limb size of *H. naledi*.

Relative limb size is a size-based limb proportion measure and is calculated using joint size and long bone robusticity. It is different from length-based proportions such as the intermembral index. Joint surfaces and long bone diaphyses are dynamic structures that respond to joint forces, muscle activity, and other mechanical demands associated with postural and locomotor behaviors. Joint surfaces and diaphyses are more robust, or larger in size, when the magnitude of mechanical loads (forces) on the bone is greater (Jungers, 1988; Aiello and Dean, 1990; Ruff and Runestad, 1992; Godfrey et al., 1995). Any change in the size of the joint, measured by the size of the articular surface or the diaphysis, will influence the relative limb size index of a species. Modern human limb proportions are driven by larger lower limb joints, which are a functional adaptation to habitual terrestrial bipedalism. This results in a derived, smaller upper to lower limb joint ratio in humans relative to great apes (Jungers, 1988). Green et al. (2007) showed a qualitative association between the higher relative limb size values of forelimb-dominant groups with higher levels of arboreality in extant apes. In addition, Gordon et al. (2020) applied dimensions of articular surfaces and diaphyses to develop a limb size index similar to relative limb size and demonstrated that this index corresponds with the extent of arboreality in extant great apes and humans.

Following these studies, we consider both articular surface and diaphyseal dimensions and broad categories of behavior such as arboreality compared to terrestriality. We apply a Monte Carlo resampling approach to estimate relative limb size in *H. naledi*, similar to the approach used by Green et al. (2007) in their consideration of *A. afarensis* and *A. africanus* limb elements. The findings of Green et al. (2007) supported the findings of McHenry and Berger (1998a), who suggested that *A. africanus* had relatively larger upper limbs that were more similar to those of apes, whereas *A. afarensis* had upper to lower limb size proportions more like modern humans. The higher, more apelike relative limb size in *A. africanus* suggests a morphological response to greater mechanical loading of the upper limbs (Green et al., 2007). Behaviorally, the contrast in relative limb size between these two species suggests that in addition to bipedalism, *A. africanus* performed activities that required this greater loading more than *A. afarensis*, including arboreal behaviors (Green et al., 2007).

Most phylogenetic analyses align *A. africanus* more closely with modern humans relative to *A. afarensis* based on shared, derived craniodental elements (White et al., 1983; Strait et al., 1997; Dembo et al., 2015). The greater similarity in relative limb size between *A. afarensis* and modern humans implies homoplasy in the evolution of limb proportions in these lineages (McHenry and Berger, 1998a; Prabhat et al., 2021). We adapt the Green et al. (2007) resampling method to generate a distribution of relative limb size values for *H. naledi* and compare this to a modern human distribution to better understand the locomotor repertoire and phylogenetic history of *H. naledi*. Based on previous research on the humanlike relative length proportion of *H. naledi* (Garvin et al., 2017) and the humanlike relative limb size proportion of LES 1 (Prahbat et al., 2021), we predict that the relative limb size of this larger sample of *H. naledi* is also humanlike. If this hypothesis is supported, it would suggest that *H. naledi* engaged in fewer positional or locomotor behaviors that required significant loading of the upper limb. Alternatively, if relative limb size is found to differ from modern humans, then this would suggest that *H. naledi* engaged in more positional or locomotor behaviors requiring significant loading of the upper limb than is seen in modern humans.

2. Materials and methods

2.1. Samples

The *H. naledi* fossil material is housed in the Philip V. Tobias Fossil Primate and Hominid Laboratory in the Evolutionary Studies Institute, University of Witwatersrand, Johannesburg, South Africa. This study includes adult long bones from both the Dinaledi and Lesedi chambers. We include measurements of 11 upper limb elements and 11 lower limb elements for a total of 22 long bone elements (21 from the Dinaledi Chamber, one from the Lesedi Chamber; Table 1).

The modern human comparative sample includes 77 adult individuals attributed to Zulu ethnicity (41 males and 36 females) from the Raymond A. Dart Collection housed at the University of

Table 1
The *Homo naledi* sample sizes and accession numbers for the elements that preserved the six linear measurements included in this study.[a,b]

Measurement	Sample size	Accession number
Diameter of radial head (RADTV)	2	U.W. 101-1346
		U.W. 101-935
Diameter of femoral head (FEMHEAD)	2	U.W. 101-1300
		U.W. 101-271
Radial midshaft circumference (RADC)	7	U.W. 101-1346
		U.W. 101-935
		U.W. 101-317 + 027
		U.W. 101-1405
		U.W. 101-1285
		U.W. 101-598
		U.W. 101-070
Humeral midshaft circumference (HUMC)	2	U.W. 101-283
		U.W. 102a-257
Femoral midshaft circumference (FEMC)	3	U.W. 101-268
		U.W. 101-003
		U.W. 101-012
Tibial midshaft circumference (TIBC)	6	U.W. 101-484
		U.W. 101-1288
		U.W. 101-213
		U.W. 101-973
		U.W. 101-571
		U.W. 101-500

[a] See SOM Table S1 for the measurement descriptions.
[b] See SOM Table S2 for the recorded values for the fossil elements and mean values for modern human comparative samples.

Witwatersrand in Johannesburg, South Africa, and 51 adult individuals attributed to White and Black ancestry groups (35 males and 16 females) from the William M. Bass Donated Skeletal Collection housed at the University of Tennessee in Knoxville, Tennessee, USA. All 128 individuals from the modern human comparative sample preserved the measurements of interest.

2.2. Measurements

Based on the preservation of the *H. naledi* material, six linear measurements of articular surfaces and diaphyses were included in this study (Table 1). To evaluate joint size, we used two measurements that have been previously defined and used by McHenry and Berger (1998a) and Green and colleagues (2007): the transverse diameter of the radial head (RADTV) and the diameter of the femoral head (FEMHEAD; Supplementary Online Material [SOM] Table S1). These diameters were measured with carbon-fiber calipers to the nearest 0.1 mm. To evaluate long bone robusticity, rather than using cross-sectional diaphyseal dimensions used by McHenry and Berger (1998a) and Green et al. (2007), we used midshaft circumferences (White et al., 2011). These also have been shown to strongly correlate with long bone robusticity (Stock and Shaw, 2007) and have the added benefit of being linear measurements so that all measurements in the study are of the same dimensionality. Midshaft circumferences were recorded for the humerus (HUMC), radius (RADC), femur (FEMC), and tibia (TIBC; SOM Table S1). Circumference was recorded with nonstick, flexible, stretch-resistant tape that was wrapped around the long bone shaft. A pencil mark was made where the end of the tape overlapped the part wrapped along the bone and using a ruler, the length from end of the tape to the pencil mark was recorded to the nearest 0.1 mm. Bony elements were primarily recorded from the left side of the body. If bones from the left side were unavailable or not well preserved, bones from the right side were recorded. Similarly, if the mediolateral diameter of the radial head was not preserved, the anteroposterior diameter was recorded. All human skeletal measurements and most fossil measurements were taken by one author (S.T.; SOM Table S2). The remaining fossil measurements were taken from the literature (Feuerriegel et al., 2017; Hawks et al., 2017; Marchi et al., 2017; SOM Table S2).

2.3. Statistical method

We replicated the Monte Carlo resampling procedure developed and validated by Green et al. (2007). For ease of replication, we used the same nomenclature as Green et al. (2007). All statistical analyses in this study were performed with RStudio v. 2.1 running R v. 4.3.1 (R Core Team, 2014).

The resampling procedure is as follows. For each measurement, we sampled with replacement the number of times equal to the *H. naledi* sample size. For example, there are two RADTV measurements, one for U.W. 101-1346 and one for U.W. 101-935. Thus, for each iteration of the analysis, we sampled with replacement two RADTV measurements. We then calculated the geometric mean (GM) of those two measurements to determine a mean RADTV measurement (mRADTV). We repeated those two steps for each measurement. We then calculated the GM of all upper limb mean measurements to establish the overall size of the upper limb (i.e., the forelimb GM, FLGM). We also calculated the GM of all lower limb mean measurements to establish the overall size of the lower limb (i.e., the hindlimb GM, HLGM). We used the natural logarithm (ln) of FLGM:HLGM to generate a mean relative limb size index value (mean RLSI), which is a measure of relative size between the upper and lower limbs. We repeated this procedure 5000 times to generate a distribution of mean RLSI values as follows:

1) FLGM = (mRADTV) × (mHUMC) × (mRADC) ^ (1/3).
2) HLGM = (mFEMHEAD) × (mFEMC) × (mTIBC) ^ (1/3).
3) Mean RLSI = ln(FLGM/HLGM).

We performed three separate resampling procedures to generate three mean RLSI distributions. One procedure used only the Dart Collection individuals to generate a mean $RLSI_z$ distribution from a single population (Zulu) to eliminate the possibility that results reflect intercontinental population structure. Another procedure used the modern human sample (including both the Dart and Bass Collection individuals) to generate a mean $RLSI_s$ distribution for a human sample that includes multiple populations. Like Green et al. (2007), we compared each actual sample mean to the resampled mean to confirm that the resampling method accurately represents the known mean of a sample, even

Table 2
Actual and resampled mean relative limb size index (RLSI) and standard deviation (SD) values for each modern human and fossil sample. Individual mean relative limb size index (RLSI) values can be calculated for modern human samples because they contain individuals with associated elements. Note that the actual means of both Dart (Zulu) and Dart and Bass human samples are within 0.001 natural log units of the resampled means.

Variable	Modern humans Dart (Zulu)	Modern humans Dart and Bass	*H. naledi*
Actual mean $RLSI_z$ (SD)	−0.571 (0.039)		
Resampled mean $RLSI_z$ (SD)	−0.571 (0.039)		
Actual mean $RLSI_s$ (SD)		−0.571 (0.043)	
Resampled mean $RLSI_s$ (SD)		−0.572 (0.044)	
Resampled mean $RLSI_n$ (SD)			−0.556 (0.022)

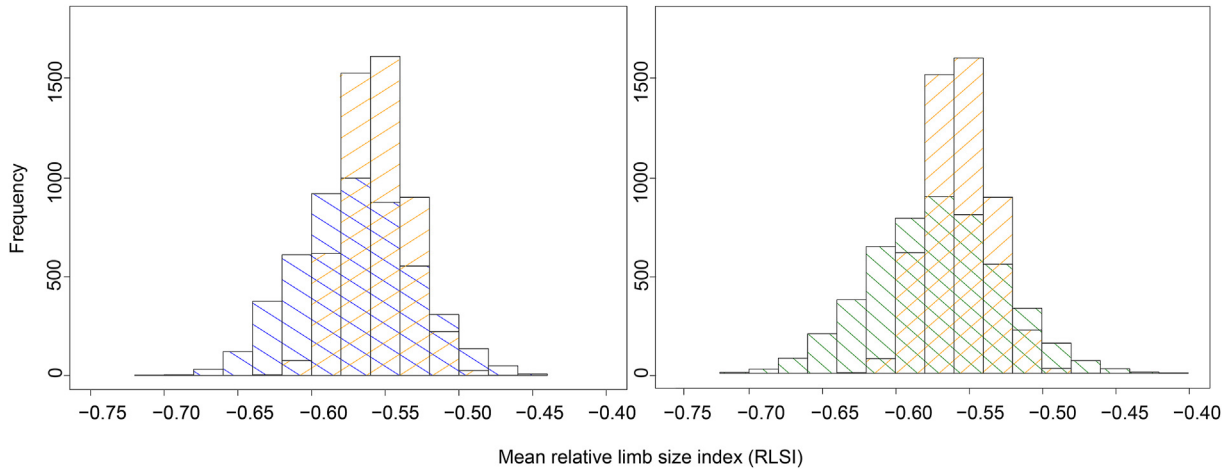


Figure 1. Histograms of resampled mean relative limb size index (RLSI) values for *H. naledi* and modern human samples. Left histogram is the *H. naledi* $RLSI_n$ distribution (orange left to right upward diagonal lines) with a mean of −0.556 (SD = 0.022) overlapping with the Dart (Zulu) comparative sample $RLSI_z$ distribution (blue left to right downward diagonal lines) with a mean of −0.571 (SD = 0.039). Right histogram is the same *H. naledi* $RLSI_n$ distribution (orange left to right upward diagonal lines) overlapping with the larger, combined Dart (Zulu) and Bass comparative human sample $RLSI_s$ distribution (green left to right downward diagonal lines) with a mean of −0.572 (SD = 0.044). (For interpretation of the references to color in this figure, the reader is referred to the Web version of this article).

when sampling restrictions are imposed. From this, we can infer that the resampling method should produce a reasonable estimate of the relative limb size in *H. naledi*, despite the fragmentary and commingled nature of the fossil remains. Once the method was validated with the comparative samples, we performed the final resampling procedure with the *H. naledi* sample to generate a mean $RLSI_n$ distribution for *H. naledi*.

Once the mean RLSI distributions were generated ($RLSI_z$, $RLSI_s$, and $RLSI_n$), we performed significance tests for pairwise comparisons of mean RLSI between *H. naledi* and the two modern human samples using a randomization procedure, again following the methods of Green et al. (2007). This procedure randomly paired a mean $RLSI_n$ value with a mean $RLSI_z$ or $RLSI_s$ value and calculated the difference [mean $RLSI_n$ − mean $RLSI_z$; mean $RLSI_n$ − mean $RLSI_s$]. We performed 5000 pairwise comparisons to generate a distribution of values equal to the difference in species' means. A difference of zero indicated that the paired RLSI values were equal. For a two-tailed t-test of significance (alpha = 0.05), the *p*-value is equal to the proportion of values less than or equal to zero multiplied by two. Our null hypothesis is that relative limb size does not differ between *H. naledi* and modern humans.

3. Results

Actual mean RLSI values and standard deviations were calculated for two modern human samples: a single population sample containing only the Dart (Zulu) individuals ($RLSI_z$), and a larger multipopulation sample containing both Dart and Bass Collection individuals ($RLSI_s$; Table 2). The actual mean $RLSI_s$ value (−0.571) is within 0.001 natural log units of the actual mean $RLSI_z$ value (−0.571). These values show that the two comparative samples are similar in their mean relative limb size. Likewise, resampled mean

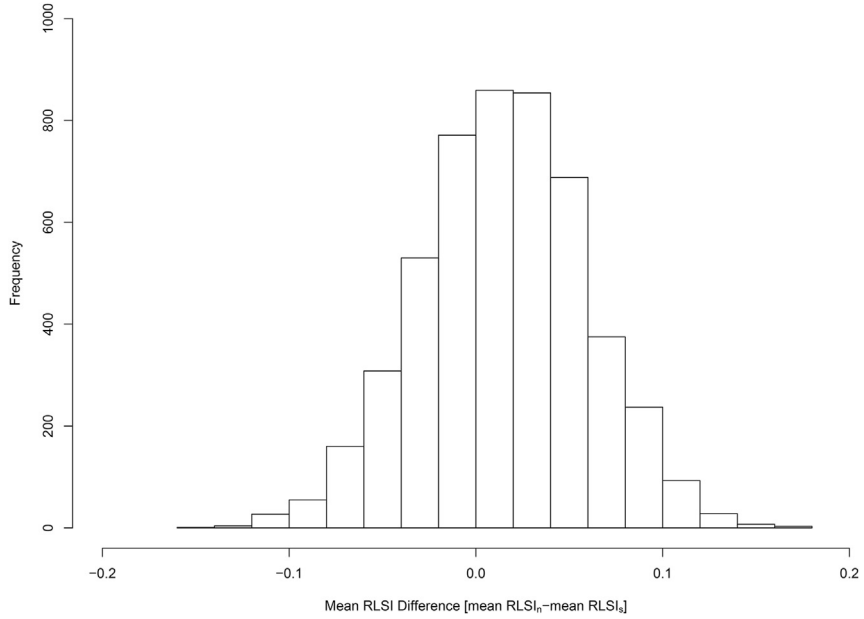


Figure 2. Pairwise comparison of mean relative limb size index difference [mean $RLSI_n$ value − mean $RLSI_s$ value]. A difference of zero indicates equal RLSI values between the two species. The difference between the two species is not significant ($p = 0.74$).

RLSI values were within 0.001 natural log units of the actual mean RLSI values for both human samples, confirming that the resampling method captures the central tendency of the samples (Table 2).

The resampling procedure generated three resampled mean RLSI distributions: two modern human distributions ($RLSI_z$ and $RLSI_s$), and one *H. naledi* distribution ($RLSI_n$). As seen in Figure 1, the *H. naledi* distribution falls within both modern human distributions. The *H. naledi* distribution ($RLSI_n$) mean (−0.556; SD = 0.022) falls well within one standard deviation of the Dart (Zulu) $RLSI_z$ (mean = −0.571; SD = 0.039; Fig. 1; Table 2) and combined Dart (Zulu) and Bass $RLSI_s$ distributions (mean = −0.572; SD = 0.044; Fig. 1; Table 2). Notably, the standard deviation of the *H. naledi* distribution is smaller than that of modern humans. Because the width of the RLSI distribution reflects, in part, the extent of sexual dimorphism in a sample, this result is compatible with other evidence that the level of body size dimorphism within *H. naledi* was low (Garvin et al., 2017).

Two significance tests for pairwise species mean difference were performed. The pairwise difference in mean relative limb size between *H. naledi* and modern humans is not statistically significant. The mean relative limb size of *H. naledi* is not significantly different from that of the Dart (Zulu) sample of modern humans ($p = 0.73$) nor is it significantly different from that of the larger Dart (Zulu) and Bass sample of modern humans ($p = 0.74$; Fig. 2). Thus, our resampled estimate of relative limb size in *H. naledi* is statistically indistinguishable from that of modern humans. These results also demonstrate that the intercontinental population structure differences between the Dart and Bass individuals do not influence the results of the study.

4. Discussion and conclusions

This study compared distributions of mean relative limb size indices from unassociated elements of *H. naledi* with two comparative samples of modern humans. The pairwise difference in mean relative limb size between the two species is not statistically significant. The *H. naledi* mean value of −0.556 is marginally higher than the human distribution mean of −0.572, reflecting a slightly greater relative upper limb size in this sample of *H. naledi* compared to the human mean. These results confirm the estimate based on the partial skeleton, LES 1 (Prabhat et al., 2021). Previous investigations of relative limb proportions in fossil hominins have inferred locomotor habits based on the relative limb size (McHenry and Berger, 1998a; Green et al., 2007; Gordon et al., 2020; Prabhat et al., 2021). Our results suggest that *H. naledi* was similar to modern humans in being lower limb dominant, implying they engaged in fewer locomotor behaviors that required significant loading of the upper limb. This affirms that bipedality was likely the most significant mode of locomotion in *H. naledi* and is in agreement with previous studies of lower extremity elements (Harcourt-Smith et al., 2015; Friedl et al., 2019; Traynor et al., 2019; Walker et al., 2019).

In contrast, other morphological investigations of *H. naledi* have highlighted apelike characteristics, which have been previously cited as evidence for climbing activities in australopiths. For example, *H. naledi* presents primitive shoulder (Feuerriegel et al., 2017), hand (Kivell et al., 2015), and foot (Harcourt-Smith et al., 2015) features consistent with arboreal behaviors. A more humanlike RLSI in *H. naledi* does not imply that *H. naledi* did not engage in arboreal behaviors, just like a more humanlike RLSI in *A. afarensis* does not preclude arboreal activity (Green et al., 2007; Prabhat et al., 2021). The mosaic limb morphology displayed by *H. naledi* may have been the result of the independent evolution of relatively larger lower limb joints due to increased reliance on bipedality (Young et al., 2010), or the result of *H. naledi*—with more humanlike joint proportions—adapting to and performing climbing activities.

Our RLSI values are not directly comparable with those presented in Green et al. (2007) or Gordon et al. (2020), but both of those studies showed *A. afarensis* to be statistically indistinguishable from modern humans and significantly more lower-limb dominant than the nonhuman great apes and *A. africanus*. Despite differences in samples and elements used in these studies, the similar upper to lower limb size ratios documented here between *H. naledi* and modern humans are notable. A more extensive comparative study would enable further testing of the hypothesis that relative limb proportions among *H. sapiens*, *H. naledi*, and *A. afarensis* are similar, as apart from the more forelimb-driven proportions of nonhuman great apes and *A. africanus*.

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Supplementary Online Material

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