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Fluctuating and Directional Asymmetry in the Long Bones of Captive Cotton-Top Tamarins (*Saguinus oedipus*)

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ABSTRACT

Objectives: Skeletal asymmetries reflect developmental stability and mechanical, functional, and physiological influences on bone growth. In humans, researchers have documented the greatest limb bone bilateral asymmetry in diaphyseal breadths, with less asymmetry in articular and maximum length dimensions. However, it remains unclear as to whether the pattern observed for humans is representative of nonhuman primates, wherein bilateral loading may minimize directional asymmetry. This study adds to the small body of asymmetry data on nonhuman primates by investigating patterns of long bone asymmetry in a skeletal sample of *Saguinus oedipus* (cotton-top tamarin).

Materials and Methods: Humeri, radii, ulnae, femora, and tibiae of 76 adult captive cotton-top tamarin skeletons (48 males, 28 females) were measured bilaterally. We included maximum length, midshaft diaphyseal breadths, and at least one articular measurement for each bone to assess directional (DA) and fluctuating asymmetry (FA) in each dimension.

Results: Most dimensions exhibit significant FA, and very few have significant DA; DA is limited to the lower limb, especially in knee dimensions. Overall, the magnitudes of asymmetry in tamarins have a consistent ranking that follows the same pattern as found in humans.

Discussion: This first study of DA and FA among multiple dimensions throughout the limbs of a non-hominoid primate suggests that previously-reported patterns of human bilateral asymmetry are not exclusive to humans. The results further indicate potential underlying differences in constraints on variation within limb bones. While processes shaping variation await further study, our results argue that different long bone dimensions may reflect dissimilar evolutionary processes. Am J Phys Anthropol 160:41–51, 2016.

Bilateral symmetry is thought to be adaptive for vertebrates since it has been linked, both theoretically and empirically, to a variety of measures of fitness (Møller, 1997). Increased levels of asymmetry are associated with sources of stress during development (Brown et al., 1989; Swaddle and Witter, 1994), increased parasitism and predation (Møller, 1996; Thornhill and Møller, 1997), and potentially lower survivorship (Novak et al., 1993). Functionally, symmetry is important for the bilateral coordination of limb movement during locomotion. Thus, it appears that mechanisms that decrease asymmetry are selectively advantageous (Gangestad and Thornhill, 1999).

Departures from symmetry have the potential to elucidate the role developmental, mechanical, genetic, and physiological factors play in growth and development (Hallgrímsson et al., 2002; Willmore et al., 2005). Numerous studies have documented a consistent asymmetry in human upper limb bones, with right side elements typically being larger, while lower limb bones tend to be more symmetric (reviewed in Auerbach and Ruff, 2006). Asymmetry, which consistently favors one side across a population, is referred to as directional asymmetry. Additionally, there appears to be a consistent pattern of directional asymmetry within skeletal elements across human populations (Auerbach and Ruff, 2006). Diaphyseal measurements display the greatest directional asymmetry, followed by articular dimensions, and lengths display the lowest levels of directional asymmetry. The absolute asymmetries provided by Auerbach and Ruff (2006) also present the same pattern, and may be used as proxies for fluctuating asymmetry, small random deviations from symmetry that do not consistently favor one side (Palmer, 1994).

The uniform patterns within human limb bones may have broader implications for the ability of traits within limbs to evolve, as reduced fluctuating asymmetry indicates greater developmental stability (Hallgrímsson

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Additional Supporting Information may be found in the online version of this article.

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et al., 2002). Developmental stability is one mechanism that buffers developmental processes against perturbations and serves to decrease variation. Research to date has largely focused on limb lengths to examine developmental stability (e.g., Hallgrímsson, 1999; Hallgrímsson et al., 2003), leaving open the question of differences in stability among traits within limbs. If the pattern of fluctuating asymmetry among limb dimensions is consistent among primates with long-divergent evolution, we would conclude that a hierarchy exists in the developmental stability of traits within bones. While the stability of a trait may not perfectly reflect its evolvability (Hansen and Houle, 2008), greater developmental stability does have implications for the ability for traits to respond to selection (Møller and Swaddle, 1997; Hallgrímsson et al., 2002).

To examine indicators of developmental stability within limbs, here we examine patterns of asymmetry in the cotton-top tamarin (*Saguinus oediupus*) to determine if human patterns are present in non-hominoid taxa, which in turn would suggest a broader pattern among primates. We selected tamarins because they are quadrupedal primates without documented species-wide patterns of asymmetry (Diamond and McGrew, 1994; Gangestad and Thornhill, 1999; Papademetriou et al., 2005; Chapelain et al., 2006; Smith and Thompson, 2011; cf. Hook and Rogers, 2002); this, coupled with the use of all limbs during locomotion, argues against an expectation of significant directional asymmetry. By examining patterns of fluctuating asymmetry among limb dimensions in tamarins, we investigate whether the broader pattern of variation among limb dimensions indicated by studies on humans is present in a monkey species.

ASYMMETRY

Patterns of asymmetry within a population are commonly described as one of three types: directional asymmetry (DA), fluctuating asymmetry (FA), and antisymmetry (AS) (Van Valen, 1962; Palmer et al., 1993). These types of asymmetry are distinguished based on the shape of the distribution of differences between sides of bilateral traits (i.e. right-left).

Directional asymmetry characterizes consistent greater development of one side of the body among individuals in a population. The distribution of differences between sides is normally distributed with a mean that differs significantly from zero (Van Valen, 1962; Palmer and Strobeck, 2003). As a species, humans preferentially use the right upper limb (Ambrose, 2001), and many skeletal studies have argued that lateralized behaviors among humans (e.g. handedness) lead to the differences in bone size and shape between sides, especially of the upper limb (Trinkaus et al., 1994; Ruff, 2000; Steele, 2000; Lieberman et al., 2001, 2003; Kontulainen et al., 2003; Auerbach and Ruff, 2006; Auerbach and Raxter, 2008; Lazenby et al., 2008a,b; Fatah et al., 2012; Ireland et al., 2013). Directional asymmetry provides researchers with the opportunity to examine the effects of different mechanical loading regimes, as it is hypothesized that genetic, hormonal, climatic, and nutritional factors affect both sides equally. Directional asymmetry may be easier to detect in the upper limb of modern humans because the limb has been decoupled from load bearing during habitual locomotion (Sylvester, 2006), allowing non-locomotor behaviors to become the dominant loading regime. An important caveat to this observation, however, is that not all lateralized behaviors will be reflected by skeletal asymmetry, as variation in the developmental stage and the duration, frequency, and magnitude of loads associated with specific lateralized tasks will have unequal effects on bone asymmetry (Ruff et al., 2006; Ubelaker and Zarenko, 2012).

Together, antisymmetry and fluctuating asymmetry are known as nondirectional asymmetry (nDA), and are characterized as asymmetry with no population-level directional bias (Palmer, 1994). More specifically, FA is asymmetry that arises from the inability of individual organisms to develop perfectly along a predetermined path (Van Valen, 1962) and can be detected as a distribution of differences between sides (i.e. right–left) that is normally distributed around a mean of zero (Palmer, 1994) with a nonzero variance. It represents a measure of “developmental noise” or minor deviations from an ideal symmetric developmental program (Van Valen, 1962; Palmer and Strobeck, 1986). Deviations from symmetry within an individual are stochastic with respect to side, but patterns within a sample can be used to infer levels of developmental stability for the character. Hallgrímsson et al. (2002) found that FA in fetal mice is correlated with heritability, suggesting that there are mechanisms in place to reduce phenotypic plasticity for some features. Based on this logic, researchers have examined independence in patterns of FA to establish independent developmental modules within skeletal elements (e.g., Klingenberg et al., 2003), as well as establish genetic and environmental factors that affect development (Sciulli et al., 1979; Leamy and Klingenberg, 2005).

Antisymmetry arises from a mechanism similar to DA, in which individuals are lateralized for particular behaviors, but differs in that the population does not show a bias towards one particular side (Van Valen, 1962). Antisymmetry will have a distribution of differences between sides centered about a mean of zero, but will either be platykurtic or in extreme cases will exhibit a bimodal distribution with each peak representing either the left-dominant or right-dominant portion of the population (Van Valen, 1962). Fluctuating asymmetry is best assessed after ruling out the presence of both DA and AS (Palmer, 1994; Kujanová et al., 2008), and although FA is ideally normally distributed, it often manifests as a leptokurtic distribution (Gangestad and Thornhill, 1999; Babbitt, 2006). Palmer (1994) argues that determining whether nDA is FA or AS is a crucial step in asymmetry analyses.

Research in the last twenty years indicates that bone does not react uniformly throughout an element to asymmetric loading (Lieberman et al., 2003). While directional asymmetries in bones are present in maximum lengths, articular breadths, and diaphyseal measures, it has been noted that diaphyseal measures are the most asymmetric (Biewener and Bertram, 1994; Auerbach and Ruff, 2006). The reason for this difference within elements is attributed by these authors to differences in canalization and/or developmental stability of the traits. Both canalization and developmental stability refer to the tendency of a developmental process to follow a particular trajectory (Hallgrímsson et al., 2002). Canalization refers to the tendency of a specific genotype to follow the same phenotypic trajectory under varied developmental and environmental influences; developmental stability refers to the tendency of a specific genotype to follow the same phenotypic trajectory under constant developmental and environmental influences. In this context, bone maximum lengths and articular sizes appear to be more developmentally stable within an individual and more canalized among populations. External diaphyseal breadths are shown to have the most variance of limb bone measures among individuals (e.g., Auerbach and Ruff, 2006) and throughout growth (Ruff et al., 1991; Lieberman et al., 2001; Ruff, 2007; Cowgill, 2010). This is likely a result of bone apposition that accommodates variation in mechanical loading patterns among and within individuals.

LIMB ASYMMETRY IN NONHUMAN PRIMATES

In part spurred by interest in the evolution of human handedness, there is a large body of literature focusing on behavioral laterality in nonhuman primates. Unlike humans, however, which clearly show a species-level right-side bias for behaviors (i.e. handedness, after McGrew and Marchant (1997)), the result for nonhuman primates are equivocal. In a meta-analysis of 48 studies, McGrew and Marchant (1997) concluded that there was insufficient evidence to support lateralization in nonhuman primates. This general finding is supported by field studies (Marchant and McGrew, 1996; McGrew and Marchant, 2001; Corp and Byrne, 2004) and captive data (Palmer, 2002).

By contrast, task-specific handedness has been documented among several species, including *Rhinopithecus roxxellana* (Zhao et al., 2012), *Cebus apella* (Spinozzi et al., 1998), *Gorilla gorilla* (Hopkins, 2008; Meguerditchian et al., 2010; Hopkins et al., 2011), and *Pan troglodytes* (Lonsdorf and Hopkins, 2005; Bogart et al., 2012). Olsen and Sommer (2014) reviewed 24 studies on hand use in callitrichid monkeys, all of which detected hand preference (biased hand use within individuals and tasks), although only two detected handedness. In short, the question of population-level handedness among nonhuman primates remains an area of considerable debate, although it seems absent in callitrichids (Hopkins, 2008; Olsen and Sommer, 2014).

While a substantial literature exists on behavioral laterality among nonhuman primates (e.g., Boesch, 1991; Hopkins, 1993; McGrew and Marchant, 1997; Lacreuse et al., 1999; Hopkins and Bard, 2000; Hopkins et al., 2005, 2011; Marchant and McGrew, 2007, 2013), fewer studies have investigated skeletal asymmetries, and skeletal asymmetries in nonhuman primates are also less well established than those in humans. An early study by Schultz (1937) documented absolute asymmetries of humeral and radial length in gorillas, chimpanzees, and orangutans, finding asymmetry to be smaller than humans. Much later, Dhall and Singh (1977) documented a right-side dominance in most of the muscles and skeletal elements of the upper limb of rhesus macaques, a finding supported by other researchers (Falk et al., 1988; Helmkamp and Falk, 1990). Morbeck et al. (1994) did not find clear patterns in the asymmetry of bone lengths, areas, weights, or mineralization for six known Gombe chimpanzees. In a study of 189 catarrhine postcrania, Buck et al. (2010) found greater variation in forelimb measures than those of the hindlimb and in diaphyses relative to articular dimensions. Hallgrímsson et al. (2002) detected greater variation and greater FA in the distal elements of rhesus macaque limbs compared to proximal elements. Sarringhaus et al. (2005) and Stock et al. (2013) demonstrated that chimpanzees have mixed patterns of DA in the upper limb: a left-biased asymmetry in humeral diaphyseal breadth and right-biased asymmetry in the midshaft of the second metacarpal. Additional nonhuman primate skeletal studies, which consider fluctuating and directional asymmetries throughout long bones, are needed to determine whether the patterns of asymmetry noted for humans are unique.

To address the questions indicated in the review above, we examine both directional and fluctuating asymmetries in three sets of dimensions in the quadrupedal, nonlateralized cotton-top tamarin: bone maximum lengths, articular dimensions, and external diaphyseal breadths. As noted above, we expect no DA in any of these dimensions among the tamarins. However, we anticipate FA to have the same pattern in tamarins as has been reported for DA in humans, where diaphyseal asymmetries are much greater than articular and length asymmetries, and that length asymmetries will be the smallest in magnitude. Given the quadrupedal nature of tamarin locomotion, as well as greater limb integration among monkeys, we furthermore do not expect differences in FA between the upper and lower limbs.

METHODS

Sample and measurements

One limitation for studies of limb asymmetries in nonhuman primates is the rarity of large skeletal samples that preserve all elements of interest. Access to a large primate sample, such as the Oak Ridge Small Primate Collection curated at The University of Tennessee, provides an opportunity to assess variability within and between limb dimensions of nonhuman, non-ape primates. The animals were part of a pedigreed colony raised at the Oak Ridge Associated Universities (ORAU) Marmoset Research Center (Clapp and Tardif, 1985). The colony was initiated in 1961 by importing animals from the wild, with a total of 451 cotton top tamarins imported from 1961 to 1981 (Cheverud et al., 1993); approximately one-third of these wild-caught tamarins reproduced as part of the breeding program established at ORAU, where every effort was made to enhance outbreeding, with mating pairs selected based on genealogy and compatibility (Clapp and Tardif, 1985; Cheverud et al., 1993).

Clapp and Tardif (1985) provide the most detailed description of the housing and breeding conditions for this sample and describe the facility as a large all-weather enclosure with 40 family-unit apartments with two interconnected 0.9 × 0.9 × 1.5 m wire mesh cage sections suspended 0.6 m from the floor. The enclosure was heated during cold months, and humidity was controlled via exhaust fans in the roof to remove moisture or a sprinkler system to produce moisture. Each family-unit apartment was provided with water ad libitum, a 17.8 × 20.32 × 40.6 cm removable nest box, and small diameter tree substrate. Animals were fed twice per day on a diet of bananas, applesauce, monkey chow, and dietary supplements (Clapp and Tardif, 1985).

During their time at the ORAU Marmoset Research Center, the tamarins were used in experimental studies, especially the examination of colon cancer (Clapp et al., 1985). However, as explored elsewhere (Hutchison and Cheverud, 1995), these studies were limited to adults, and so should not have affected the development of the limb bones during ontogeny, when environmental effects have the greatest influence on bone shape and size. Individuals with evidence of disease were excluded from the study. In our sample of 76 adult cotton-top tamarins (*Saguinus oedipus*; 48 males, 28 females), 24 were wild-caught, 38 were born in captivity to wild-caught parents, 10 were born in captivity to one wild-caught parent and one captive-born parent, and four were offspring of two captive-born parents. In all cases of animals born to captive-parents, pedigree information indicated descent from independent wild-caught lineages, arguing that inbreeding should have minimal impact on estimates of asymmetry.

Twenty-nine limb dimensions were measured bilaterally by one of us (N.M.R.) for humeri, ulnae, radii, femora, and tibiae (Fig. 1) of each individual. Skeletal dimensions were selected to assess the relative magnitudes of asymmetry in length, articular, and diaphyseal dimensions in light of the patterns previously reported among humans. The maximum length, midshaft anteroposterior (AP) and mediolateral (ML) diaphyseal breadths, as well as at least one articular measurement were included for each bone to compare these types of dimensions. Maximum lengths were taken using a Paleo-Tech mini-osteometric board. Diaphyseal midshaft positions (50% of maximum length), and the AP and ML breadths at the midshaft were collected using Mitutoyo Digimatic 150 mm (sliding) calipers. Articular dimensions for these nonhuman primates were chosen after Ruff (2002) and were collected with the same digital sliding calipers. All measurements were taken to the nearest 0.01 mm. Metacarpals and phalanges were not included in the study because their small size made it difficult to obtain reliable mid-shaft and articular dimensions (although lengths were generally measurable and repeatable). Since the goal was to include each type of dimension (length, articular and diaphysis) for each bone, measurement difficulties precluded including hand and finger bones.

All dimensions were measured three times each over several weeks by the same researcher (N.M.R.). These repeated measurements were used to estimate measurement errors for all dimensions (Supporting Information Table SI1), which were calculated by averaging the absolute deviations of each measurement from the mean of the three trial measurements, then expressing this mean deviation as a percentage of the mean measurement. Most dimensions are considered to have high precisions, with measurement errors less than 1% for most dimensions, and less than 3% for all dimensions.

Analyses

Before assessing sources of asymmetry, male and female skeletal measurements (average of sides within each individual specimen) were compared using ANOVA tests to decide if the sexes should be analyzed separately or pooled. Asymmetry values for wild-caught and captive-born specimens were also compared using ANOVA tests before pooling all specimens for asymmetry analyses. Asymmetry was examined following Palmer (1994) by subtracting the left measurement from the right side measurement, and differences were converted into percentages by dividing by their average value using the following equation:

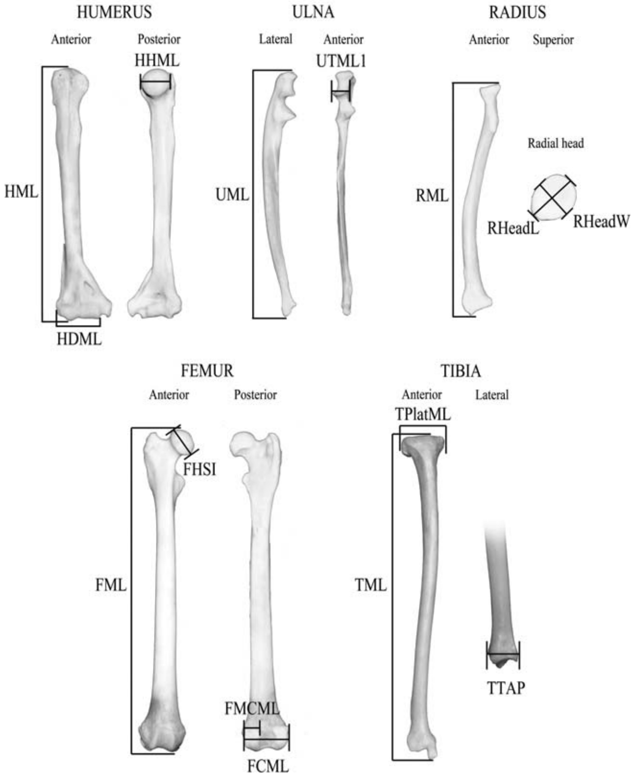

Fig. 1. Limb dimensions of tamarin long bones used in this analysis. Midshaft AP and ML breadths for each bone, RCML, RCAP, FMCSI, FLCSI are not pictured. Pictures not to scale. See Ruff (2002) for more detailed depictions of generalized primate bones; abbreviations correspond with this publication.

$$\%\text{Asymmetry} = (R-L)/((R+L)/2) \times 100$$

Percent asymmetry indicates the magnitude and direction of biases, with positive values for right-biased asymmetries and negative values for left-biased asymmetries.

Potential sources of total asymmetry (DA, FA, and AS) were assessed by procedures outlined by Palmer and Strobeck (1986), Palmer (1994), and Palmer and Strobeck (2003), which have been used by other researchers to assess asymmetry in a variety of species (Klingenberg and McIntyre, 1998; Klingenberg et al., 2003; Trotta et al., 2005; Willmore et al., 2005). To address the potential confounding effect of AS in assessing FA, the distributions of differences between sides (i.e. R-L) were checked for normality using conventional skewness and kurtosis statistics (Sokal and Rohlf, 1987; Palmer and Strobeck, 1992; Palmer, 1994). Confidence intervals (99% confidence limits) for kurtosis and skewness statistics were generated using a bootstrap procedure with 1,000 iterations of resampling with replacement, followed by kurtosis and skewness estimates. Ninety-nine percent confidence intervals were employed to guard against Type I errors given the large number of variables. Departures from normality were indicated by confidence intervals for skewness statistics that did not include zero and for kurtosis values that did not include the value three. In the absence of departures from normality, nDA may be interpreted as FA (Palmer, 1994).

Directional and nondirectional asymmetry (nDA) were assessed using a two-factor mixed model ANOVA, with "individual" as a random factor and "side" as a fixed factor, after Palmer and Strobeck (1986), Palmer (1994), and Merila and Biorklund (1995). This approach partitions the variances into several sources: The "individual" animals (variation is size and shape among the animals), "side" (systematic differences between side, i.e. DA), the interaction between "individual" and "side" (nDA), and measurement error.

The effect of trait size (e.g. bone length vs. articular dimensions) on the estimate of FA was removed by natural log-transforming all raw data measurements to obtain size-scaled measures of FA (Wright, 1952; Van Valen, 1978; Palmer and Strobeck, 2003; Willmore et al., 2005). The presence of DA can be tested using the factorial ANOVA approach using an F-test, with $F = \mathrm{MS}_{\mathrm{side}}/\mathrm{MS}_{\mathrm{side} \times \mathrm{individual}}$ (Palmer, 1994) which determines if the mean difference between sides is greater than expected given the amount of nDA. Nondirectional asymmetry was also tested with an F-test, with $F = \mathrm{MS}_{\mathrm{side} \times \mathrm{individual}}/\mathrm{MS}_{\mathrm{measurement\ error}}$, and asks if the amount of nDA is greater than expected given the amount of measurement error. This second test was only conducted if the test for DA was nonsignificant (Palmer, 1994).

Palmer and Strobeck (2003) provide several indexes for estimating FA. Descriptors of FA estimate a variance because FA is recognized by a distribution of between side differences (R–L) centered around zero with a nonzero standard deviation. Several FA indexes use the standard deviation of the between side differences to estimate FA (e.g. Palmer and Strobeck (2003) FA4a, FA5a, FA6a). Fluctuating asymmetry can also be estimated as the mean of the absolute value of between side differences, which can be size scaled by the individual or the sample. Fluctuating asymmetry estimators that utilize the absolute values of the differences between sides (|R-L|) flip the left side of the distribution (below zero) onto the right side. The mean of this strongly asymmetric distribution is tightly linked with the distribution variance, hence also providing a measure of FA (e.g. Palmer and Strobeck (2003) FA1, FA2, FA3). For normal distributions, the expected mean of the asymmetric distribution of absolute values differs from the standard deviation of the signed distribution by a constant $(2/\pi)^{0.5} = 0.798$ (Kendall and Stuart, 1951; Palmer and Strobeck, 2003). In the present study, FA was estimated using Palmer and Strobeck's (2003) FA10b index, which uses the partitioned mean sum of squares (MS) from the ANOVA and is calculated using the following formula where M represents the number of measurement replicates:

$$\mathrm{FA10b} = 0.798 \times (2 \times (\mathrm{MS}_{\mathrm{side} \times \mathrm{individual}} - \mathrm{MS}_{\mathrm{measurement\ error}})/M)^{1/2}$$

The advantage of this approach is that variance attributed to measurement error, which can inflate measures of nDA, is subtracted from the variation attributed to nDA. As discussed, the leading constant (0.798) makes the above index (FA10b) comparable to indexes based on the mean of absolute values of between side differences. This is also true of the internal constant (Palmer and Strobeck, 1986; Palmer, 1994). This approach describes the total nDA as a proportion of the trait mean after partitioning out measurement error (following Palmer and Strobeck, 1986; Palmer, 1994; Fields et al., 1995; see also Palmer and Strobeck, 1997). Alpha values were set at 0.01 for all tests to guard against Type I errors, however no sequential Bonferroni correction was used for these F-tests in order to maximize the statistical power available for these analyses and minimize Type II errors (Perneger, 1998). Original measurements and calculations were performed using Microsoft Excel 2011 for Apple Macintosh. All statistical analyses were performed using built-in statistical procedures in Matlab.

RESULTS

Means and standard deviations for the 29 bone dimensions by side are provided in Table 1. Twenty-eight of the 29 measurements have measurement errors less than 2.0%[1] (Supporting Information Table SI1). Closer examination of the measurements reveals a general pattern in the percent error values. The smallest dimensions, articular sizes and diaphyseal diameters, have the highest measurement errors. Consequently all errors are considered to have negligible effects on the further analyses, especially as the FA10b index takes measurement error into consideration, and all twenty-nine dimensions were analyzed for sources of asymmetry.

Individual ANOVA tests indicate that for all 29 traits, there was not a significant difference between the male and female measurements ($P > 0.01$; Table SI2). This is unsurprising, as cotton-top tamarins do not exhibit sexual dimorphism in size (Savage et al., 1993). In addition, analyses did not reveal differences between wild-caught and captive-born specimens in asymmetry values ($P > 0.01$; Supporting Information Table SI3). Consequently data for wild-caught and captive-born specimens were also pooled for further analysis.

Asymmetry

Skewness and kurtosis values for all distributions of differences between measurements of sides (i.e. R-L) are provided in Table 2. None of the 29 bone measurements displayed significant departures from normality as the 99% confidence intervals for all traits includes the value 0 for skewness and the value 3 for kurtosis (Table 2).

Mean and median percent asymmetries for the total sample, with sexes pooled, are presented in Table 3. Mean values range from a minimum of −1.13% (indicating the left side is larger) for the superoinferior dimension of the lateral femoral condyle to a maximum of 2.65% (indicating a right side bias) for the anteroposterior dimension of the radius midshaft. For most measurements, the median percent asymmetry has the same sign as the mean value, but this is not the case for all dimensions. For humerus maximum length, ulna mediolateral diaphyseal midshaft and radius mediolateral diaphyseal midshaft, the mean value is positive (suggesting a right bias) while the median is negative (indicating a left bias). These findings indicate that there are more individual tamarins with a left bias for these measurements, but for those tamarins with a right bias, the bias is of a greater average magnitude. None of the measurements showed the reverse trend.

The two-factor mixed model ANOVA and the resulting F-tests indicate that directional asymmetry is present in

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[1] The mediolateral midshaft diaphyseal measurement of the ulna is the only dimension with an error greater than 2% on average; this measurement imprecision is likely attributable to the difficulty of orienting the bone and the small magnitude of the dimension (mean = 1.83 mm, 1.82 mm; $s = 0.22$ mm; 0.21 mm), which is the smallest measurement taken in this study.

TABLE 1. Means and standard deviations for long bone dimensions by side

		Mean (mm)		Std. Dev. (mm)	
Bone	Measurement	Right	Left	Right	Left
Humerus	HML	51.22	51.20	1.56	1.56
	HHML	6.27	6.19	0.27	0.25
	HDML	8.57	8.60	0.32	0.31
	H50AP	3.82	3.84	0.23	0.23
	H50ML	3.89	3.86	0.27	0.27
Ulna	UML	53.88	53.86	1.92	1.92
	UTML1	3.88	3.92	0.19	0.19
	U50AP	3.54	3.51	0.25	0.26
	U50ML	1.83	1.82	0.21	0.22
Radius	RML	46.44	46.38	1.74	1.86
	RheadL	4.83	4.83	0.20	0.20
	RHeadW	3.85	3.85	0.14	0.15
	RCML	5.31	5.32	0.17	0.18
	RCAP	3.07	3.03	0.17	0.16
	R50AP	2.38	2.32	0.18	0.16
	R50ML	2.77	2.75	0.22	0.23
Femur	FML	66.29	66.24	2.10	2.06
	FHSI	6.07	6.09	0.28	0.27
	FCML	9.39	9.43	0.25	0.25
	FMCML	3.21	3.19	0.18	0.17
	FMCSI	5.61	5.56	0.17	0.17
	FLCSI	5.58	5.64	0.17	0.17
	F50AP	4.18	4.09	0.23	0.22
	F50ML	4.23	4.21	0.23	0.22
Tibia	TML	67.22	67.05	2.26	2.13
	TPlatML	9.42	9.47	0.27	0.26
	TTAP	4.58	4.62	0.20	0.19
	T50AP	4.33	4.29	0.27	0.25
	T50ML	3.10	3.12	0.17	0.18

eight of the bone dimensions measured (*P* values <0.01; Table 4). Two are measurements of the radius (anteroposterior diameter of the midshaft and the anteroposterior distal radius articular diameter), four are measurements of the femur (anteroposterior diameter of the midshaft, superoinferior dimension of both condyles, and femoral bicondylar breadth), and two are measurements of the tibia (maximum length and mediolateral diameter of the plateau). For those measurements that do exhibit DA, there is a general trend of percent asymmetry in which lengths exhibit the lowest amount of asymmetry, followed by articular dimensions, and midshaft dimensions have the largest percent asymmetry values. This is true even when all bones are considered together.

Nondirectional asymmetry (nDA)

In contrast to the results of statistical tests for the presence of significant DA among the limb bone dimensions, results calculated from the mixed-model ANOVAs indicate that significant nondirectional asymmetries are present in almost all other measurements; these are presented in Table 4. Of all the dimensions for which the test for nDA was conducted (those that exhibited no DA) only the humeral head diameter does not have a statistically significant nDA (i.e. asymmetry that cannot be distinguished from measurement error). The significant nDA values can be interpreted as FA because earlier tests do not indicate departures from normality. Also included in Table 4 are the size-scaled estimates of FA for each bone dimension, as well as their rank values (within a bone). In the upper limb, there is a very clear trend of increasing FA in which maximum lengths

TABLE 2. Skewness and kurtosis values for all distributions of differences between measurements of sides (i.e. right-left)

Bone	Measurement	Type of measure	Skew (99% CI)		Kurtosis (99% CI)	
Humerus	HML	Max. Length	−0.28	0.97	2.09	4.21
	HHML	Prox. Articular	−0.14	1.03	2.13	4.95
	HDML	Dist. Articular	−0.79	0.42	2.05	4.25
	H50AP	Diaphysis	−0.8	0.84	2.6	4.99
	H50ML	Diaphysis	−0.67	0.43	1.91	4.12
Ulna	UML	Max. Length	−1.95	1.62	2.97	10.08
	UTML1	Prox. Articular	−0.22	1.01	2.17	4.58
	U50AP	Diaphysis	−0.47	0.39	1.82	3.08
	U50ML	Diaphysis	−1.42	0.56	2.15	5.97
Radius	RML	Max. Length	−0.85	2.03	2.34	11
	RheadL	Prox. Articular	−0.76	0.86	2.33	5.04
	RHeadW	Prox. Articular	−0.83	1.28	2.48	6
	RCML	Dist. Articular	−0.72	0.91	2.65	4.77
	RCAP	Dist. Articular	−0.65	1.07	1.8	5.41
	R50AP	Diaphysis	−0.72	2.68	1.91	16.22
	R50ML	Diaphysis	−3.02	2.45	2.44	18.47
Femur	FML	Max. Length	−0.64	1.22	2.75	6.47
	FHSI	Prox. Articular	−0.98	0.33	1.82	4.68
	FCML	Prox. Articular	−0.48	3.1	1.86	19.46
	FMCML	Dist. Articular	−0.26	0.57	1.93	3.56
	FMCSI	Dist. Articular	−0.92	0.52	2.09	4.55
	FLCSI	Dist. Articular	−0.25	0.79	2.11	3.78
	F50AP	Diaphysis	−0.8	0.5	1.93	4.19
	F50ML	Diaphysis	−0.58	0.45	2.04	3.57
Tibia	TML	Max. Length	−0.06	1.36	2.27	5.47
	TPlatML	Prox. Articular	−0.3	0.61	1.79	3.07
	TTAP	Dist. Articular	−0.76	1.37	2.78	6.77
	T50AP	Diaphysis	−0.75	1.55	2.13	8.04
	T50ML	Diaphysis	−0.42	0.74	2.11	4.03

TABLE 3. Mean and median percent asymmetries for the total sample ($N = 76$)

Bone	Measurement	Mean difference right–left side (mm)	Mean unsigned difference right–left side (mm)	%DA mean	%DA median
Humerus	HML	0.02	0.32	0.044	−0.074
	HHML	−0.01	0.10	−0.169	−0.105
	HDML	−0.04	0.14	−0.426	−0.306
	H50AP	−0.02	0.10	−0.399	−0.546
	H50ML	0.02	0.09	0.634	0.744
Ulna	UML	0.02	0.28	0.033	0.037
	UTML1	−0.04	0.11	−1.019	−0.619
	U50AP	0.03	0.10	0.990	0.540
	U50ML	0.01	0.09	0.301	−0.001
Radius	RML	0.05	0.30	0.129	0.194
	RHeadL	−0.01	0.05	−0.099	−0.141
	RHeadW	0.00	0.05	0.070	0.169
	RCML	0.00	0.09	−0.032	−0.374
	RCAP	0.04	0.10	1.235	1.078
	R50AP	0.06	0.10	2.647	2.650
	R50ML	0.02	0.11	0.591	−0.062
Femur	FML	0.06	0.33	0.086	0.123
	FHSI	−0.02	0.06	−0.265	−0.396
	FCML	−0.04	0.11	−0.442	−0.509
	FMCML	0.02	0.10	0.643	0.345
	FMCSI	0.05	0.09	0.969	1.181
	FLCSI	−0.06	0.10	−1.130	−1.093
	F50AP	0.10	0.13	2.341	2.188
	F50ML	0.02	0.07	0.388	0.231
Tibia	TML	0.17	0.41	0.246	0.207
	TPlatML	−0.05	0.10	−0.541	−0.595
	TTAP	−0.03	0.10	−0.766	−0.829
	T50AP	0.03	0.10	0.705	0.483
	T50ML	−0.02	0.06	−0.630	−0.792

TABLE 4. Limb asymmetry values and statistics

Bone	Measurement	Type of measure	Significant DA *P* value	FA (rank within bone)
Humerus	HML	Max. Length	0.64	**0.0064 (1)**
	HHML	Prox. Articular	0.48	0.0091
	HDML	Dist. Articular	0.07	**0.0112 (2)**
	H50AP	Diaphysis	0.29	**0.0233 (3)**
	H50ML	Diaphysis	0.05	**0.0222 (4)**
Ulna	UML	Max. Length	0.71	**0.0062 (1)**
	UTML1	Prox. Articular	>0.01	**0.0235 (2)**
	U50AP	Diaphysis	0.02	**0.0270 (3)**
	U50ML	Diaphysis	0.66	**0.0448 (4)**
Radius	RML	Max. Length	0.23	**0.0074 (1)**
	RheadL	Prox. Articular	0.57	**0.0115 (2)**
	RHeadW	Prox. Articular	0.73	**0.0126 (3)**
	RCML	Dist. Articular	0.90	**0.0163 (4)**
	RCAP	Dist. Articular	**<0.01**	0.0240
	R50AP	Diaphysis	**<0.001**	0.0318
	R50ML	Diaphysis	0.35	**0.0414 (5)**
Femur	FML	Max. Length	0.28	**0.0054 (1)**
	FHSI	Prox. Articular	0.06	**0.0091 (2)**
	FCML	Dist. Articular	**<0.01**	0.0097
	FMCML	Dist. Articular	**0.13**	**0.0264 (4)**
	FMCSI	Dist. Articular	**<0.001**	0.0092
	FLCSI	Dist. Articular	**<0.001**	0.0111
	F50AP	Diaphysis	**<0.001**	0.0190
	F50ML	Diaphysis	0.17	**0.0191 (3)**
Tibia	TML	Max. Length	**<0.01**	0.0060
	TPlatML	Prox. Articular	**<0.001**	0.0084
	TTAP	Dist. Articular	>0.01	**0.0094 (1)**
	T50AP	Diaphysis	0.04	**0.0163 (2)**
	T50ML	Diaphysis	0.04	**0.0199 (3)**

Bold values are significant ($P < 0.01$).

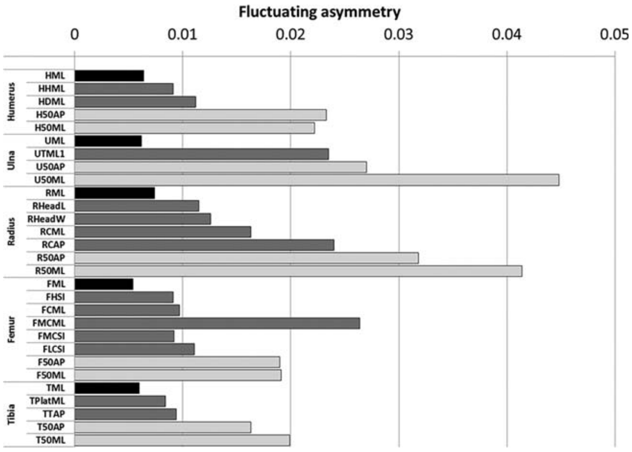

Fig. 2. Fluctuating asymmetry of limb dimensions.

exhibit the least FA, followed by proximal articular dimensions, distal articular dimensions, and finally midshaft dimensions with the greatest FA values. The trend was also generally true of the hind limb elements, with the exception of the femur in which bicondylar width exhibits the greatest amount of FA. Thus, the following general pattern emerges for magnitudes of FA within tamarin long bones (from smallest to greatest): maximum lengths, proximal articular size, distal articular size, and diaphyseal midshaft diameters (Fig. 2).

DISCUSSION

As this is the first time that patterns of all types of asymmetry have been examined in multiple dimensions of the limbs in a nonhominoid primate, expectations were set using human patterns for relative magnitudes of asymmetry among limb dimensions. With regard to asymmetry within a bone (i.e. comparing length, articular dimensions, diaphyseal dimensions) these results show that patterns of asymmetry in tamarins are similar to those published for humans (Trinkaus et al., 1994; Auerbach and Ruff, 2006; Auerbach and Raxter, 2008). Diaphyseal breadths have the most DA or FA in the limbs, and generally, maximum lengths have the least asymmetry either in terms of DA or FA. Articular surface measurement asymmetry measures fall in between these other two classes of dimensions. The exception to this general pattern was that the mediolateral width of the femoral condyles expressed more FA than did the midshaft (Table 4, Fig. 2).

Contrary to the hypothesis set out in the Introduction, there is population-wide DA found for some limb dimensions, especially diaphyseal breadths and distal articulation size, and this was largely found in the lower limb skeletal elements. The source of skeletal asymmetry in the radius is unknown as the literature suggests that tamarins are not lateralized at the population or species level (i.e. handedness), like humans (Olsen and Sommer, 2014). Before considering the implications of these results further, it is important to point out that none of the asymmetry observed exceeds 0.5 mm in total (absolute) deviations (Table 3). Given the small magnitude of most limb bone dimensions these deviations may be biologically consequential for the tamarins, though any such assertions are speculative. Thus, more emphasis is placed on patterns of asymmetry among the limb bone dimensions in the analysis of these results.

Unlike humans, the majority of the significant DA values for the tamarins occur in the lower limb. This result is somewhat unexpected given the quadrupedal locomotion of the tamarins, although Hook and Rogers (2002) demonstrate that common marmosets may use left and right limbs consistently for specific roles during leaping behaviors. Since there are only six measurements of the lower limb that exhibit directional asymmetry, it is difficult to discern a particular pattern. Four of the measurements are articular dimensions, three of which show a left side bias (femoral bicondylar width, superoinferior dimension of the lateral condyle, and the mediolateral width of the tibial plateau). These three measurements are consistent with one another, making it hard to ascribe the pattern to an artifact of sampling; taken together these suggest the left knee is, overall, larger. The fourth articular measurement (superoinferior dimension of the medial condyle) is biased to the right side, thus opposite of the general knee trend and may reflect differences in the angle between the distal femur and proximal tibia. Of the other two dimensions showing DA, one is a diaphyseal measurement (anteroposterior diameter of the femur) and the other, the maximum length tibia, is the only bone to show a length DA, and both are biased to the right side. While the DA of tibial length is significant, it appears to be driven mainly by six captive-born individuals with highly asymmetric tibiae (>1.4% of mean bone length). If these six specimens are removed from the analysis the test for DA becomes nonsignificant ($P > 0.05$).

The most important conclusion drawn from the analyses of asymmetry, in light of the hypotheses set out in the introduction, is that tamarin long bones follow a pattern of asymmetry similar to those reported for humans (Auerbach and Ruff, 2006). Regardless of the association of these results with specific lateralized behavior or other factors, the identical pattern of asymmetry is noteworthy for additional discussion. Moreover, the pattern of FA in the limb bones supports this finding, and has important implications for developmental stability within the limb bones of primates, as well as the relationship of DA and nDA.

The magnitudes of asymmetry and the pattern of significant FA in the tamarin sample suggest a consistent ranking in the amount of asymmetry in long bone dimensions. Coupled with results from previous studies on other primates, this ranking may reflect general patterns of developmental instability among primate limbs. Simply, variance in the diaphyseal external dimensions is less constrained than the variance in external articular dimensions or lengths. If this variance were an indicator of potential evolution of the limb—as phenotypic variance should be proportional to genetic variance (Steppan et al., 2002; Roseman and Auerbach, 2015)—then it suggests that limb bone lengths and articular dimensions are evolutionarily constrained relative to diaphyseal dimensions. Our study, however, does not take a quantitative genetic approach, and so we cannot extrapolate more about evolution from our results; future studies using quantitative evolutionary genetic models should look into canalization and evolvability of different dimensions within limbs. Furthermore, the universality of the pattern of magnitudes of asymmetry among primate limb dimensions should be assessed with more taxa across the order.

Our results do argue further for independence in the development of long bone lengths and diaphyseal breadths. The findings in general support the hypothesis that long bone lengths are more developmentally stable and less responsive to local effects of activity than diaphyseal measures, a finding now borne out in multiple studies (Biewener and Bertram, 1994; Lieberman et al., 2003; Auerbach and Ruff, 2006; Auerbach and Raxter, 2008; Auerbach et al., 2010; Fatah et al., 2012). Functional constraints resulting from locomotion may be one factor driving this pattern, but differences in the regulation and apposition of bone between sides may also serve a more fundamental governing role in the maintenance of limb bone length symmetry (Hallgrímsson et al., 2003). Diaphyseal dimensions, in contrast, must adjust to loading behavior throughout life in order to resist mechanical stresses (e.g., Ruff et al., 2006; but see Wallace et al., 2014), and while this allows for greater flexibility in local responses—and therefore higher amounts of asymmetry compared with all other external dimensions—diaphyses still maintain a general pattern of development and correspondence between limb elements, at least in humans (Cowgill, 2010; Ruff et al., 2013).

The moderate asymmetry in articular surfaces bears additional attention. The correspondence of patterns and magnitudes of both fluctuating and directional asymmetries between functionally related articular dimensions is likely due to the fact that they must conform within the same side, and affect each other in development (Carter and Beaupré, 2001). A new finding in this study, however, is that asymmetry in external articular dimensions increases distally; and both the FA and DA show this pattern. Safety factors of bone (a ratio of fracture stress to peak functional stress, that is, how “over engineered” a bone is (Biewener, 1983)) have been documented to decrease distally along limbs (Alexander, 1981; Young et al., 2014), and patterns of bone functional adaptation likewise differ between the proximal and distal cortices of limb bones (Lieberman et al., 2003). Whether these biomechanical aspects of limb bones correspond with the proximodistal pattern in asymmetry cannot be made, however the link among them is compelling; it is possible that the distal portions of bone are more sensitive to their mechanical environment than proximal portions, and therefore lead to more asymmetry (Lieberman et al., 2003). It is also possible that differences in shape and joint motion in distal relative to proximal articulations are an important factor driving this pattern. An examination of asymmetry in the trabecular bone in these articulations would further illuminate this pattern, as trabecular bone is more responsive to loading after the end of primary growth than the cortical shells of articulations (Ruff et al., 1991; Plochocki et al., 2006).

Finally, this study shows correspondence between the patterns of magnitudes between directional and fluctuating asymmetries. It is difficult to compare the residual variance of FA analyses with the scaled percentages calculated from arithmetic differences in dimensions for DA analyses. Other studies have suggested the possibility of the presence of developmental noise within measures of DA (e.g., Markow, 1992; Graham et al., 1993). Palmer (1994) and Palmer and Strobeck (2003) argue that asymmetries are additive not only in a statistical sense, but biologically as well. This is the first study to demonstrate similar patterns of asymmetry among primate limb dimensions for both directional and fluctuating asymmetry. Future studies should address the interaction between these by experimentally assessing developmental instability in the limbs and the manifestation of asymmetry types.

In conclusion, the pattern of DA and FA within individual limb bones of tamarins matches that of DA published for humans, but is distinguished from the human pattern in that the hind limb skeletal elements of tamarins are more asymmetric. These results support a generalized model of limb bone development where different dimensions of each limb bone show varying amounts of stability, as well as independence from each other. The more asymmetric measures of the diaphyses suggest that they have greater variance, are likely more developmentally plastic, and might be better indicators of an individual’s behavior. In contrast, the more symmetric articular and length dimensions may be more developmentally stable and/or canalized, and potentially would be useful for classifying or interpreting the evolution of locomotor behaviors and phylogenetic relationships.

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