Title: Long Legs and Short Arms: Development and the Evolvability of Human Limbs **Authors**: N.M. Young, G.P. Wagner, B. Hallgrímsson

Supplementary Information

PNAS PNAS

Correlation Magnitude, Structure and the Relationship to Population Variance

Initial resampling of our data suggested that in highly integrated datasets estimated correlations vary with the sampled population variance. We hypothesized that this is because if two traits are highly correlated then increasing the sampled variance will improve the estimated correlation, whereas if the correlation is low then increasing the sampled variance will not improve correlation estimates. This artifact between correlations and variance has important ramifications for the comparison of integration, because it implies that there is a significant risk of both Type I and Type II errors when statistically comparing mean estimates of integration between populations. For example, if one group has a higher estimated variance than a second, significant differences in integration between them could be due to either: (i) a real difference in integration, or (ii) an artifact of differences in sample variance. Only the former is meaningful for studies of integration while the latter indicates that conclusions from comparative studies of integration are likely to be flawed without correction.

To better understand this relationship, we conducted a simulation in which we generated known covariance structures in limb data. To generate these data, we took a factor-based approach. The value for each limb element was calculated as the sum of normally distributed deviations associated with four hypothetical variance sources added to an assumed population mean and scaled by an assumed population variance. In our simulations, we used the sample means and variances from the macaque data as the starting point. The value for each element was thus calculated as:

$$LV_{E} = \mu_{E} + \left(\left(\left(W_{Org} \times N_{Org} \right) + \left(W_{Limb} \times N_{Limb} \right) + \left(W_{SH} \times N_{SH} \right) + \left(W_{LE} \times N_{LE} \right) \right) \times \sigma_{E} \right)$$

Where:

 μ_{E} = assumed population mean for that limb element

 σ_E = assumed population standard deviation for that limb element

 W_{Org} = proportion of variance determined by organism-wide variation in size W_{Limb} = proportion of variance determined by limb-specific variation in size W_{SH} = proportion of variance determined by serially homologous element-specific variation in size

 $W_{\mbox{\tiny LE}} = \mbox{proportion}$ of variance determined by limb element-specific variation in size

N = a normally distributed random number with a variance of one and mean of zero

In this simulation, there is no resampling from a larger sample. Instead, each individual within each sample is unique and generated *de novo* using the method described above.

We used this basic scheme to conduct two different simulations. In the first, we generated 380 samples of 50 individuals for ten different hypothetical covariation structures (total N = 190,000) that varied in the strength of each of the four factors. Out of the ten hypothetical covariation structures, six generated the effect of significant correlation of VE with population variance (here we use the trace of the covariance matrix, but similar results obtain with other measures such as the average CV%). These results are shown in **Supplementary Figure 1**. Covariation structures that did not exhibit the effect either had a single covariation determinant or very large element-specific variance. The former is unrealistic and the latter produces essentially random correlation matrices, which is also not characteristic of biological data. Within the six remaining covariation structures that generated the effect, the correlation for a log-linear regression between VE and sample variance ranged from 0.47 to 0.82, while the slope and intercept also varied. This result led us to hypothesize that the magnitude of the observed effect is dependent on covariation structure.

To further explore how covariation structure determines the nature of this sampling artifact, we examined all possible combinations of covariation structures possible within our scheme, varying the proportional contribution of each covariance factor in increments of 0.2. For each of the 58 possible combinations, we generated 50 samples of 50 individuals and calculated the VE (from the correlation matrix) and the sample variance. We next obtained the correlation between VE and the trace for each run of 50 samples per covariance structure. Analysis of these correlations showed that the strength of the artifact depends both on the average VE for that covariation structure and on the number of covariance generating factors (**Supplementary Figure 2**). Significantly, the most realistic biological model of covariance involves four factors and also exhibits the strongest effect.

This simulation demonstrates that there is a positive correlation between VE and the sample variance and that this relationship depends on covariation structure. In other words, the sampling error of VE and the sampling error of the population variance are correlated under conditions that are similar to those encountered in real biological datasets (**Supplementary Figure 3**). The implication of this finding for the comparative analysis of integration is that when the covariance structures of the samples being compared are broadly similar, this relationship can be taken into account in order to make appropriate comparisons. This is the approach taken in our study. Pairwise matrix correlations are significant between all taxa, with the exception of *Saimiri*, although this species is not significantly different than either *Homo* or *Macaca* (**Supplementary Table 2**).

Supplementary Figure Legends:

Supplementary Figure 1: The relationship between the variance of the eigenvalues (VE) and the sample variance (trace of the variance-covariance matrix) for six hypothetical covariance structures as determined by simulation. For each covariance structure, 380 random populations (N = 50) were generated, and the VE plotted against population variance. For each simulated covariance structure VE exhibited a significant log-linear relationship with sample variance although the correlation, slope, and intercept varied on the structure.

Supplementary Figure 2: Summary results for the simulation demonstrating the dependence of the VE variance artifact on the number of factors generating covariance structure. Each data point represents the mean VE and the Fisher's-*z* transformed correlation (population variance versus VE) for a simulation run (N = 50) with a given covariance structure (range = one to four factors). This simulation demonstrates that the strength of the artifact depends on the VE as well as the number of covariance generating factors. The most realistic model of four factors exhibits the strongest relationship.

Supplementary Figure 3: A comparison of resampled distributions (1,000 replicates with $r_m > 0.95$) of four alternative partitions of the Homo dataset: (i) the raw data (green), (ii) the raw data mean-centered for ethnicity and sex differences (purple), (iii) the centered data pruned of individuals outside the 95% confidence limit (orange), and (iv) the residuals of the raw data regressed on trunk length (blue). Each partition has statistically indistinguishable covariance structure (inset: r_m adjusted for repeatability below diagonal, p-values above, matrix repeatability along the diagonal) yet differ in the population variance sampled. Log-linear regression estimates for a VE at a common population variance (4%) yields consistent values (range = 1.79 - 2.15, mean = 1.94) using both within partition regressions (colored circles) and an estimate using a regression from all of the data (i.e., "Total", regression shown as dashed line). In order to be consistent across species datasets where information on body size is not available, we report VE estimates from the centered data. This analysis shows that while the population variance affects the magnitude of correlation estimates under real sampling conditions, this relationship is predictable and therefore correctable when comparing population integration among populations or species. This relationship also holds for both estimates of individual and average correlations.

2.789, $r^2 = 0.671$; Gorilla gorilla: VE = $ln(CV) \cdot 2.756 - 1.856$, $r^2 = 0.564$; Hylobates lar: VE = $ln(CV) \cdot 3.296 - 2.766$, $r^2 = 0.441$; Macaca mulatta: VE = $ln(CV) \cdot 2.867 - 0.898$, $r^2 = 0.772$; Trachypithecus cristatus: VE = $ln(CV) \cdot 2.931 - 0.497$, $r^2 = 0.736$; Saimiri sciureus: VE = $ln(CV) \cdot 3.071 - 1.552$, $r^2 = 0.714$; Aotus trivirgatus: VE = $ln(CV) \cdot 3.333 - 1.369$, $r^2 = 0.533$).

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Enocios	Sar	nple Siz	e	Popul	ation Vari	ance (Average	trait coef	ficient	of variation [C	V])
species	Female	Male	Total	Humerus	Radius	Metacarpal	Femur	Tibia	Metatarsal	Mean
Homo sapiens	62	71	133	5.27	6.10	5.65	5.86	6.31	6.21	5.90
Pan troglodytes	26	21	46	4.64	5.63	6.60	4.33	5.37	6.75	5.56
Gorilla gorilla	20	42	62	4.06	4.41	5.21	4.41	4.97	5.36	4.74
Hylobates lar	31	32	63	3.55	3.76	4.79	3.75	4.36	4.32	4.09
Macaca mulatta	93	83	176	3.78	4.26	4.96	4.27	4.35	4.35	4.33
Trachypithecus cristatus	42	17	59	3.04	3.15	4.58	3.24	3.06	4.10	3.53
Saimiri sciureus	60	42	102	4.51	4.06	5.88	5.02	5.13	5.36	4.99
Aotus trivarigatus	21	53	74	3.38	3.35	2.88	3.78	4.07	3.54	3.50

Supplementary Table 1: Descriptive statistics of each sample.

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Supplementary Table 2: Matrix correlations (below diagonal [values scaled by repeatability]), matrix repeatability (diagonal [autocorrelation of 10,000 replicates)¹, and significance value of the matrix correlation (above diagonal [Mantel's test, 10,000 replicates]) for pairwise comparisons of all species.

Species	Ното	Pan	Gorilla	Hylobates	Масаса	Trachypithecus	Saimiri	Aotus
Ното	0.945	0.011	0.008	0.013	0.003	0.005	0.015	0.018
Pan	0.908	0.907	0.021	0.010	0.025	0.008	0.128	0.010
Gorilla	0.841	0.768	0.948	0.000	0.029	0.039	0.195	0.008
Hylobates	0.891	0.905	0.999	0.950	0.017	0.035	0.150	0.005
Масаса	0.872	0.798	0.699	0.810	0.970	0.000	0.045	0.011
Trachypithecus	0.902	0.882	0.637	0.774	0.972	0.934	0.075	0.024
Saimiri	0.618	0.324	0.306	0.341	0.507	0.577	0.949	0.196
Aotus	0.747	0.773	0.751	0.835	0.775	0.706	0.336	0.968

Supplementary Table 3: Estimated correlation (below diagonal) and partial correlation (above diagonal) matrix for *Homo sapiens*.

	Humerus	Radius	Metacarpal	Femur	Tibia	Metatarsal
Humerus	1	0.188	0.260	0.368	0.088	-0.201
Radius	0.709	1	0.111	0.005	0.444	0.160
Metacarpal	0.540	0.543	1	0.109	-0.179	0.658
Femur	0.800	0.694	0.484	1	0.464	-0.179
Tibia	0.804	0.792	0.527	0.845	1	0.331
Metatarsal	0.480	0.586	0.726	0.412	0.578	1

Supplementary Table 4: Estimated correlation (below diagonal) and partial correlation (above diagonal) matrix for *Pan troglodytes*.

	Humerus	Radius	Metacarpal	Femur	Tibia	Metatarsal
Humerus	1	0.005	0.101	0.446	0.227	-0.107
Radius	0.593	1	0.303	0.111	0.316	0.177
Metacarpal	0.327	0.608	1	0.233	-0.375	0.638

Femur	0.805	0.686	0.399	1	0.551	0.054
Tibia	0.712	0.677	0.225	0.824	1	0.095
Metatarsal	0.272	0.539	0.772	0.387	0.232	1

Supplementary Table 5: Estimated correlation (below diagonal) and partial correlation (above diagonal) matrix for *Gorilla gorilla*.

	Humerus	Radius	Metacarpal	Femur	Tibia	Metatarsal
Humerus	1	0.463	0.230	0.367	0.236	-0.430
Radius	0.812	1	0.335	0.108	0.424	-0.111
Metacarpal	0.479	0.651	1	0.009	-0.306	0.803
Femur	0.717	0.733	0.544	1	0.230	0.110
Tibia	0.710	0.811	0.613	0.733	1	0.445
Metatarsal	0.161	0.383	0.778	0.246	0.467	1

Supplementary Table 6: Estimated correlation (below diagonal) and partial correlation (above diagonal) matrix for *Hylobates lar*.

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	Humerus	Radius	Metacarpal	Femur	Tibia	Metatarsal
Humerus	1	0.427	-0.272	0.567	0.085	0.047
Radius	0.730	1	0.474	0.016	0.380	-0.212
Metacarpal	0.307	0.625	1	0.128	0.039	0.732
Femur	0.794	0.709	0.440	1	0.254	-0.018
Tibia	0.700	0.783	0.527	0.722	1	0.077
Metatarsal	0.128	0.362	0.782	0.278	0.352	1

Supplementary Table 7: Estimated correlation (below diagonal) and partial correlation (above diagonal) matrix for *Macaca mulatta*.

	Humerus	Radius	Metacarpal	Femur	Tibia	Metatarsal
Humerus	1	0.132	0.084	0.505	0.210	-0.102
Radius	0.797	1	0.095	0.137	0.502	0.032
Metacarpal	0.614	0.715	1	-0.081	-0.143	0.826
Femur	0.857	0.828	0.653	1	0.259	0.137
Tibia	0.829	0.904	0.724	0.871	1	0.323
Metatarsal	0.659	0.774	0.911	0.725	0.810	1

Supplementary Table 8: Estimated correlation (below diagonal) and partial correlation (above diagonal) matrix for *Trachypithecus cristatus*.

	Humerus	Radius	Metacarpal	Femur	Tibia	Metatarsal
Humerus	1	0.242	-0.055	0.344	0.041	0.215
Radius	0.859	1	0.355	0.094	0.381	-0.182
Metacarpal	0.755	0.811	1	0.006	-0.138	0.734
Femur	0.890	0.881	0.762	1	0.550	0.028
Tibia	0.872	0.902	0.777	0.929	1	0.253
Metatarsal	0.818	0.807	0.920	0.817	0.837	1

Supplementary Table 9: Estimated correlation (below diagonal) and partial correlation (above diagonal) matrix for *Saimiri sciureus*.

	Humerus	Radius	Metacarpal	Femur	Tibia	Metatarsal
Humerus	1	0.344	0.368	0.603	-0.062	-0.055
Radius	0.699	1	-0.221	-0.161	0.442	-0.033
Metacarpal	0.733	0.448	1	0.078	-0.124	0.615
Femur	0.915	0.673	0.700	1	0.595	-0.240
Tibia	0.846	0.753	0.707	0.900	1	0.557
Metatarsal	0.704	0.550	0.817	0.695	0.810	1

Supplementary Table 10: Estimated correlation (below diagonal) and partial correlation (above diagonal) matrix for *Aotus trivirgatus*.

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	Humerus	Radius	Metacarpal	Femur	Tibia	Metatarsal
Humerus	1	0.056	-0.123	0.553	-0.032	-0.140
Radius	0.800	1	-0.193	0.096	0.568	0.366
Metacarpal	0.648	0.766	1	0.094	0.326	0.491
Femur	0.878	0.914	0.797	1	0.512	0.233
Tibia	0.833	0.935	0.810	0.951	1	-0.272
Metatarsal	0.609	0.783	0.800	0.783	0.734	1

Supplementary Table 11: Relative arm/leg lengths for ceboid, cercopithecoid and hominoids used in **Figures 1C/D** and **3A** (2).

Group	Species Common Name	Arm/Trunk	Leg/Trunk	Arm/Leg
	Bald-headed tamarin	111.7	110.0	101.5
	True marmoset	98.4	94.8	103.8
	Marmoset	100.2	99.7	100.5
e a	Squirrel Monkey	95.6	92.2	103.7
ide	Capuchin	119.3	115.5	103.3
ebc	Saki	118.5	115.2	102.9
Ŭ	Uakari	134.7	119.8	112.4
	Owl Monkey	103.3	100.5	102.8
	Howler Monkey	146.2	117.0	125.0
	Wooly Monkey	156.1	126.7	123.2
	Spider Monkey	184.4	135.0	136.6
	Baboon	134.4	117.0	114.9
	Celebes Macaque	145.5	129.5	112.4
g	Barbary Macaque	111.8	100.0	111.8
ide	Rhesus Macaque	114.0	100.8	113.1
000	Managabey	127.7	120.5	106.0
ithe	Vervet Monkey	100.7	96.5	104.4
do	Red guenon	107.7	101.8	105.9
ero	Langur	108.0	97.8	110.4
0	Proboscis Monkey	139.5	113.5	122.9
	Black Colobus	103.8	96.9	107.1
-	Gibbon	251.0	152.7	164.4
dea	Siamang	234.1	131.4	178.2
ioc	Orangutan	199.6	118.2	168.8
u-i-	Chimpanzee	173.5	128.3	135.2
ېد ام	Gorilla	153.7	112.4	136.7
	Human	149.1	167.2	89.2

Supplementary Table 12: Intermembral index (IMI) for gibbon, macaque, guenon and tamarin radiations used in **Figure 3B**. All data from (3-7).

Group	Species	IMI
	Hylobates agilis	130.9
	Hylobates klossii	124.0
	Hylobates lar	131.4
	Hylobates moloch	128.3
	Hylobates muelleri	130.2
	Hylobates pileatus	122.0
	Hylobates (Bunopithecus) hoolock	128.3
	Hylobates (Nomascus) concolor	142.2
Apes	Symphalangus syndactylus	145.0
	Pongo pygmaeus pygmaeus	139.0
	Pongo pygmaeus abellli	139.0
	Pan troglodytes schweinfurthi	103.0
	Pan troglodytes troglodytes	106.0
	Pan troglodytes verus	106.0
	Pan paniscus	102.0
	Gorilla aorilla aorilla	116.0
	Gorilla aorilla berinaei	116.0
Old World	Semnopithecus entellus	83.0
Monkeys	Kasi johnij	80.0
(Ouadrupeds)	Trachypithecus obscura	83.0
(, , , , , , , , , , , , , , , , , , ,	Presbytis melalophos	78.9
	Presbytis comata	76.0
	Presbytis rubicunda	76.0
	Presbytis frontata	76.0
	Presbytis hosei	75.0
	Nasalis larvatus	94.0
	Pyaathrix nemaeus	94.0
	Mandrillus sphiny	95.0
	Panio hamadruas	95.0
	Panio anubis	95.0
	Papio cupocophalus	97.0
	Papio Lynocephalas	90.0
	Papio ursinus Therepithesus colada	90.0
	Macaca diapus	100.0
	Macaca pomostring	92.0
	Macaca tenkeana	98.0
	Macaca tonkeana	95.0
		100.0
	Macaca brunnecens	99.0
	Масаса пескі	93.0
	Macaca nigra	84.0
	Macaca assamensis	96.0
	Macaca thibetana	95.0
	Macaca arctoides	98.0
	Macaca fasicularis	93.0
	Macaca mulatta	93.0
	Cercocebus agilis	84.0
	Cercocebus torquatus	83.0
	Cercocebus galeritus	84.0
	Lophocebus albigena	78.0
	Cercopithecus mitis	82.0
	Cercopithecus nictitans	82.0
	Cercopithecus ascanius	79.0

PNAS PNAS

	Cercopithecus cephus	81.0
	Cercopithecus mona	86.0
	Cercopithecus diana	79.0
	Cercopithecus preussi	82.0
	Cercopithecus Ihoesti	80.0
	Cercopithecus neglectus	82.0
	Colobus guereza	79.0
	Colobus polykomos	78.0
	Piliocolobus badius	87.0
	Procolobus verus	80.0
	Pithecia pithecia	75.0
	Pithecia monachus	77.0
	Chiropotes satanas	83.0
	Cacajao calvus	83.0
	Callicebus moloch	74.0
	Callicebus cupreus	77.0
F	Callicebus donacophilus	75.0
ľ	Callicebus torquatus	79.0
ľ	Callicebus personatus	73.0
	Aotus sp.	74.0
ľ	Cebus apella	81.0
ľ	Cebus albifrons	81.0
ľ	Cebus capucicus	81.0
F	Cebus olivaceus	83.0
	Saimiri sciureus	80.0
New World	Samiri oerstedii	80.0
Monkeys	Saguinus nigricollis	78.0
(Quadruped)	Saguinus fuscicollis	79.0
	Saguinus tripartitus	80.0
	Saguinus mystax	74.0
	Saguinus labiatus	73.0
ľ	Saguinus imperator	75.0
ľ	Saguinus midas	77.0
	Saguinus oedipus	74.0
ľ	Saguinus geoffroyi	76.0
ľ	Saguinus leucopus	74.0
ļ	Leontopithecus rosalia	89.0
ļ	Callithrix argentata	76.0
	Callithrix jacchus	76.0
	Callithrix aurita	74.0
	Callithrix penicillata	76.0
	Cebuella pyamaea	83.0

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Supplementary Table 13: Intermembral index (IMI) for gibbon, macaque, guenon and tamarin radiations used in **Figure 3C**.

Radiation (Estimated Divergence Time) ^A	Species ^B	Intermembral Index (IMI)	Published Data Source
Gibbons ^c	Hylobates agilis	130.9	(4)
(6-7Ma)	Hylobates klossii	124.0	This dataset
	Hylobates lar	131.4	This dataset
	Hylobates moloch	128.3	(4)
	Hylobates muelleri	130.2	(4)
	Hylobates pileatus	122.0	This dataset

	Hylobates (Bunopithecus) hoolock	128.3	(4)
	Hylobates (Nomascus) concolor	142.2	This dataset
	Symphalangus syndactylus	144.5	(4)
	Macaca silenus	92.0	(3)
	Macaca nemestrina	98.0	(3)
	Macaca tonkeana	95.0	(3)
	Macaca ochreata	100.0	(3)
	Macaca brunnecens	99.0	(3)
	Macaca hecki	93.0	(3)
Macaques	Macaca nigra	92.0	(5)
(7.6	Macaca maura	92.0	(5)
±1.3Ma)	Macaca assamensis	96.0	(3)
	Macaca radiata	91.0	(6)
	Macaca thibetana	95.0	(3)
	Macaca arctoides	98.0	(3)
	Macaca fasicularis	93.0	(3)
	Macaca mulatta	93.0	(3)
	Macaca fuscata	93.0	(7)
	Allenopithecus nigroviridis	83.0	(3)
	Cercopithecus ascanius	79.0	(3)
	Cercopithecus cephus	81.0	(3)
	Cercopithecus diana	79.0	(3)
-	Cercopithecus Ihoesti	80.0	(3)
Guenons	Cercopithecus mitis	82.0	(3)
(8.1	Cercopithecus mona	86.0	(3)
±1.0Ma)	Cercopithecus neglectus	82.0	(3)
	Cercopithecus nictitans	82.0	(3)
	Cercopithecus preussi	82.0	(3)
	Chlorocebus aethiops	83.0	(3)
	, Miopithecus talapoin	83.0	(3)
	Saguinus nigricollis	78.0	(3)
	Saguinus fuscicollis	79.0	(3)
	Saquinus tripartitus	80.0	(3)
	Saquinus mystax	74.0	(3)
Tamarins (11-16Ma)	Saguinus labiatus	73.0	(3)
	Saguinus imperator	75.0	(3)
	Saguinus midas	77.0	(3)
	Saguinus oedipus	74.0	(3)
	Saguinus geoffroyi	76.0	(3)
	Saguinus leucopus	74.0	(3)

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^AThe gibbon radiation is comparable in age to the *Pan-Homo* split ⁸, estimated at ~6-7Ma ⁹. Divergence estimates based on paleontological and molecular data indicate that macaque ^{9, 10}, and guenon ¹⁰ radiations are of approximately similar time depth. Tamarins diverged from other callitrichines in the Late to Middle Miocene ¹⁹.

^B Systematists place either all gibbon species into a single genus (*Hylobates*) ⁴, distinguish multiple subgenera within *Hylobates* (shown in parentheses) ⁸, or recognize the siamang as a separate genus (*Symphalangus*) based on size ⁵. More recently, molecular systematists have recognized as many as four gibbon genera based on behavioral, geographic, karyotypic and molecular data ¹². These generic distinctions are listed in the table parenthetically.

Supplementary References

PNAS PNAS

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Figure S1

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