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A comprehensive allometric analysis of 2^nd^ digit length to 4^th^ digit length in humans

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Abstract

It has been widely reported that men have a lower ratio of the 2nd and 4th human finger lengths (2D:4D). Size-scaling ratios, however, have the seldom-appreciated potential for providing biased estimates. Using an information-theoretic approach, we compared twelve candidate models, with different assumptions and error structures, for scaling untransformed 2D to 4D lengths from 154 men and 262 women. In each hand, the 2-parameter power function and the straight line with intercept, both with normal, homoscedastic error, emerged as relatively superior and essentially equivalent models for normalising 2D to 4D lengths. The conventional 2D:4D ratio biased relative 2D length low for the generally bigger hands of men, and *vice versa* for women, thereby leading to an artifactual indication that mean relative 2D length is lower in men than women. Conversely, use of the more appropriate allometric or linear regression models revealed that mean relative 2D length was, in fact, *greater* in men than women. We conclude that 2D does not vary in direct proportion to 4D for both men and women, rendering the use of the simple 2D:4D ratio inappropriate for size-scaling purposes and intergroup comparisons.

1. Introduction

Relative index finger length (2D:4D), calculated as the ratio between the length of the 2nd (2D) and 4th (4D) fingers, has interested researchers for more than a century [1]. In the human hand, three phenotypes have been defined: index shorter than ring finger (i.e. 2D < 4D), index and ring finger being equal in length (i.e. 2D = 4D), and index longer than ring finger (i.e. 2D > 4D) [2].

The 2D:4D ratio has been reported to be associated with a broad range of human characteristics, such as behavioural traits, fertility, handedness, sexual orientation, sex-related diseases, and sports performance [3-9], although effect sizes are generally low to moderate. Sex differences in the 2D:4D ratio have been investigated extensively [7] where men tend to have a lower 2D:4D ratio than women [10]. In an important study on mice, endocrine signalling examined during a narrow window of embryonic exposure to differential levels of androgens and oestrogens was found to be associated with the 2D:4D ratio [11]. Nevertheless, an important question is whether the index is independent of its denominator, which is an essential requirement for the accuracy of the 2D:4D ratio, and indeed any index which normalises one variable for another variable [12].

In the biological sciences, the construction of a simple ratio, of the form *Y*/*X*, is a common approach used to derive a standardized variable of an examined trait where the numerator, the criterion variable, is typically divided by a denominator, the predictor variable [12]. For example, oxygen uptake is conventionally normalised per-ratio standards to body weight in human samples [13]. Likewise, left ventricular ejection fraction is calculated as the ratio of stroke volume to end-diastolic volume and represents the traditional measure of contractility of the mammalian heart [14]. Additionally, previous studies in evolutionary biology revealed that the neocortex ratio, which is the resultant of the neocortex to brain size ratio, carries information about the number of social relationships in primates [15].

Nevertheless, the empirical and theoretical shortcomings of simple ratios as size-adjustment approaches are noteworthy [12, 13, 16-19]. Since a size-proportion ratio seldom normalises the *Y* variable consistently across the measurement range of the *X* variable [12], the unappreciated residual size-correlation inherent to ratiometric indices has, in general, led researchers to formulate untenable biological explanations [18, 19].

When a ratio is still substantially correlated with its denominator then, as we have demonstrated with a number of other physiological ratios [20], biased inferences can result. Another indicator of the inappropriateness of ratios is a substantial non-zero *Y*-intercept in the linear relationship between numerator and denominator [19], and such a non-zero intercept has been reported for 2D:4D [10, 21]. While there have been attempts to partition out the confounding effects of differences in the length of 4D to obtain unbiased interpretations of the 2D:4D ratio [21], a thorough allometric scrutiny of this morphometric index has not been published to date.

Since Julian Huxley's seminal study on the chela size of the *Uca pugnax* in 1924 [22], methods for allometric scaling have entailed, to a great extent, logarithmic transformations of the original measurements [23]. Nonetheless, logarithmic modelling might introduce an undetected systematic bias into calculations [24], and, importantly, yields a mathematical function not describing the biological relationship between the examined observations in the arithmetic domain [23]. Recent advances in the analytical procedures for studies of allometry and scaling now permit a more comprehensive appraisal of linear and non-linear regression models based on the underlying assumptions and nature of random error [25].

Therefore, we aimed to compare, using a formal information-theoretic approach, twelve candidate models for scaling untransformed 2D and 4D lengths, and ascertain how different model selections influence the quantification of sex differences in relative index finger length in humans.

2. Methods

The study sample of 416 participants comprised data collected directly by the researchers from 154 men and 262 women. The study design, methods and ethics procedures used to obtain the data have been previously described [21]. This study also adhered to the ethics and research governance procedures at Teesside University. Separate analyses were conducted for the right and left hands. Measures of centrality and dispersion were expressed as mean ± standard deviation (SD).

Type I regression procedures [26] and the analytical framework outlined in a recently published article on methods for allometric analysis [25] were used to examine the morphometric relationship between the fingers. Briefly, we performed non-linear regression analyses of untransformed observations using the Model Procedure in SAS version 9.4 to fit three sets of four models, involving two straight lines and two power functions, with multiplicative, log-normal, heteroscedastic error, and additive, normal, homoscedastic or heteroscedastic error, respectively [25]. Parameter estimates for each model were solved using an iterative protocol based on the Marquardt procedure [25]. Participants' sex was also included as a categorical covariate in the statistical models. A common slope was fitted for the whole sample when the effect of the sex × 4D interaction term was found not to be substantial. Sex differences in the slope would indicate a fundamentally different relationship between 2D and 4D and preclude comparisons between men and women [27]. The Akaike Information Criterion (AIC) was adopted to assess the relative quality of each candidate model [28]. The ΔAIC from the estimated best model (i.e. the model with the lowest AIC value; ΔAIC = 0) was judged according to the following scale: 0-2, essentially equivalent; 2-7, plausible alternative; 7-14, weak support; > 14, no empirical support [28]. Parameter estimates were interpreted from the best/essentially equivalent models for the examined data. Regression parameters are reported as point estimates and 95% confidence limits (CL). All statistical analyses were conducted using SAS (PROC MODEL, SAS® Version 9.4; SAS Institute, Inc., Cary, NC), and graphs were produced using IBM Statistical Package for the Social Sciences (SPSS) Statistics version 23.0 (SPSS, Chicago, IL).

Table 1 about here

Figure 1 about here

3. Results

As expected, mean lengths of 2D and 4D were larger in men than women, irrespective of the examined hand (Table 1). For the right hand, the substantial, inverse correlations between the 2D:4D ratio and 4D in both sexes indicated that the ratiometric index is not normalising for 4D length uniformly across the measurement range (Fig. 1a, b). The correlation coefficients (95%CL) describing the relationship between the index and its denominator were found to be -0.42 (-0.56 to -0.27) and -0.34 to (-0.45 to -0.22) in men and women respectively. The mean 2D:4D ratio was greater in women (0.993 ± 0.037) than in men (0.982 ± 0.037), with the 95%CL for this sex difference being 0.004 to 0.019.

Following our formal comparisons, in the right hand, the 2-parameter power function with normal, homoscedastic error, of the form $Y = \mathrm{a}{\cdot}X^{\mathrm{b}}$, was found to be the best out of twelve competing models (Table 2). The allometric exponent (b) describing the non-linear relationship between 2D and 4D was 0.80 (0.74 to 0.85). A ratio index is free of bias only if this exponent is 1. The 95%CL for the difference in exponent between males and females was -0.21 to 0.02. Using this most appropriate size-scaling model, women displayed a lower, and not higher, mean 2D:4D than men (Table 1). The model with straight line, intercept, and normal homoscedastic error was found to be "essentially equivalent" to the best model: $Y = 13.59 + 0.79{\cdot}X$. The 95%CL for the Y-intercept was 10.19 to 16.99. Table 2 reveals that the

3-parameter power function (relaxing the constraint of a zero *Y*-intercept in the 2-parameter model) was also “essentially equivalent”.

In the left hand, we found negative correlations between 2D:4D and 4D of similar magnitudes to those observed in the right hand (Fig. 1c, d). The correlation coefficient between the 2D:4D ratio and 4D was -0.48 (-0.62 to -0.33) in men, and -0.45 to (-0.56 to - 0.35) in women. Again, women had a greater mean 2D:4D ratio than men (0.992 ± 0.037 vs. 0.984 ± 0.036), with the 95%CL for this difference being 0.001 to 0.016. The AIC criteria revealed the rectilinear function with intercept and normal, homoscedastic error ($Y = 16.10 + 0.75 \cdot X$) to be the best model in the set of candidates (Table 3). The 95% confidence interval for the positive *Y*-intercept was 12.96 to 19.25. The 95%CL for the difference in the regression slope between the sexes was -0.17 to 0.03. The 2-parameter power function was found to be “essentially equivalent” to the best model, with an allometric exponent of 0.76 (0.71 to 0.80). The 95%CL for the sex difference in the exponent was -0.17 to 0.04. The adjusted mean 2D:4D estimates from the best / essentially equivalent models were found, again, to be lower among women than men (Table 1). In line with AIC outcomes, the model residuals were well behaved in both hands (Fig. 2).

Table 2 about here

Table 3 about here

Figure 2 about here

4. Discussion

Although the 2D:4D ratio has been selected to study the association between differences in relative index finger length and biological traits, the substantial residual dependency of the 2D:4D ratio on its denominator (4D) hinders the understanding of the true relationship between the 2D and 4D in human samples (Figure 1). Accordingly, the traditional approach of normalising 2D for differences in 4D length as simple ratio statistics fails to serve this purpose in an unbiased manner across the typical measurement range of finger lengths in both men and women.

Notably, the outcomes of the British Broadcasting Corporation (BBC) study were seemingly interpreted as an additional line of evidence supporting the description of a sexual dimorphism based on sex differences in the 4D linear regression slope [10]. Nevertheless, the *Y*-intercept value, and not the linear regression slope, is the criterion parameter in linear regression models indicating the validity of a ratio statistics [19]. Not only did the inverse association between the 2D:4D ratio and 4D we observed highlight the spurious size-dependence of the index (Figure 1), but the uncontrolled confounding effects of morphological differences in 4D length illustrated the degree of bias in 2D:4D estimates [10]. Since the underlying assumptions of ratios were found to be violated [12, 19], the notion of a sexually dimorphic index established on the previously reported sex differences in the 4D linear regression slope is, therefore, untenable.

In the human foetus, the differentiation in the growth patterns of the fingers appears at a gestational age of approximately nine weeks [29]. The mechanistic interplay between androgen and oestrogen signalling regulates the network of genes involved in chondrocyte proliferation and, therefore, the morphological relationship between the fingers [11]. Notwithstanding these mechanisms, the mathematical flaws of the 2D:4D ratio alter the magnitude of sex differences in relative index finger length and, consequently, lead to erroneous interpretations. The molecular pathways obviously shed light on the *absolute* differences in the length of the fingers between the sexes [11], whereas any interpretations about casual associations grounded on the biased size-proportion 2D:4D ratio are limited by non-biological factors introducing artifactual variability.

The large ΔAIC for the ratio standards models (straight line, no intercept) in both hands demonstrated that these models have essentially no support (Table 2 and 3). In particular, our study provides a comprehensive and novel approach for deriving 2D:4D measures standardized for differences in the 4D working directly in the raw arithmetic data space. After simple allometric or linear regression-standards normalisation, the mean 2D:4D estimates from the best models were found to be higher in men than women, irrespective of the examined hand and modelling approach (Table 1). Nonetheless, the drawbacks of power-function ratios are well-established [12]. While power-function ratios might turn out to successfully eliminate size correlations, they paradoxically introduce size-related distortions in distributional patterns compared to modelling morphometric relationships using raw data [12]. Accordingly, the adjusted 2D:4D ratios and adjusted 2D length we derived from the model residuals were both independent of 4D length and materially unaffected by distributional distortions [12]. The adjusted 2D:4D indices were derived according to the empirical and theoretical assumptions regarding the use of residuals, which reflect the true biological variability of the observed values independent of body size [12]. Our approach involved modelling the 2D:4D ratio as the dependent variable, adjusting for 4D length using the residuals method [12], and then obtaining an adjusted ratio free from the influence of 4D length. Importantly, this size-adjustment approach is mathematically equivalent to modelling 2D length as the dependent variable [30], with the advantage of providing a properly adjusted ratio index rather than an expression of 2D length free from the influence of 4D length. The mathematical equivalence and concordance between these analyses ultimately substantiate the failure of simple ratio models (Tables 2 and 3) to provide unbiased 2D:4D estimates (Figure 1) [12, 30]. Furthermore, the measurement of 2D and 4D lengths carried out by trained anthropologists is another key strength of the present study that minimizes any random variability in the examined data [21]. Our results reflect a long-standing wealth of evidence in the biological literature, whereby relationships between morphometric variables seldom vary in a directly proportional fashion [12, 13, 16-19].

We, therefore, point out that the formulation of this index as a simple ratio might cloud any potential associations between the relative length of the fingers and other human traits, particularly sex differences. To date, the formulations of simple ratios as the 2D:4D have been superseded by more comprehensive and accurate allometric analyses for addressing size-scaling problems [25]. If the relationship between the 2D and 4D was found to be directly proportional, for a given value of 4D the 2D:4D ratio would have predicted the same value of the outcome compared to what we observed after proper modelling of differences in the denominator of the index.

Our study demonstrates that, in human samples, failure to statistically control for the true covariation patterns associated with the 4D in the 2D:4D ratio provides biased estimates of differences between the sexes and, consequently, a spuriously sexually dimorphic index.

Authors' contributions

L.L., A.M.B., and G.A. contributed to the design of the paper, conducted statistical analyses, wrote, and revised the manuscript. L.K., and J.F. provided the examined data and contributed to the manuscript revision. K.L.W. contributed to the revision of the manuscript. All authors approved the final version of the manuscript and agree to be accountable for the content herein.

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Competing interests

We declare no competing interests with regard to this publication.

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Table Legends

Table 1. Descriptive characteristics of the study participants (n = 416).

Table 2. Statistical models fitted to untransformed data for scaling 2D (mm) to 4D (mm) in the right hand.

Table 3. Statistical models fitted to untransformed data for scaling 2D (mm) to 4D (mm) in the left hand.

Figure Legends

Figure 1. Scatterplots showing the negative correlation between the 2D:4D ratio and the length of the 4D for men (a, c), and women (b, d) in the right and left hand, respectively.

Figure 2. Raw residuals against the untransformed 4D measures from the 2-parameter power function (a, c), and linear regression (b, d) model with normal, homoscedastic error in the right and left hand, respectively.

Table 1. Descriptive characteristics of the study participants (n = 416)

Variable	Men (n = 154)	Women (n = 262)
Right hand		
2^{nd} finger length, mm	73.82 ± 4.19	67.77 ± 4.60
	(61.00 to 87.00)	(42.80 to 79.00)
4^{th} finger length, mm	75.27 ± 4.61	68.31 ± 4.76
	(64.00 to 89.00)	(39.80 to 79.90)
2D:4D ratio	0.982 ± 0.037	0.993 ± 0.037
2D:4D normalised index[a]	0.993 ± 0.034	0.986 ± 0.035
2D:4D normalised index[b]	0.994 ± 0.033	0.986 ± 0.035
2D:4D normalised index[c]	2.328 ± 0.079	2.310 ± 0.081
Adjusted 2^{nd} finger length, mm[a]	70.37 ± 2.40	69.79 ± 2.46
Adjusted 2^{nd} finger length, mm[b]	70.34 ± 2.51	69.82 ± 2.38
Left hand		
2^{nd} finger length, mm	74.13 ± 4.10	67.46 ± 4.36
	(61.00 to 90.00)	(44.20 to 78.00)
4^{th} finger length, mm	75.42 ± 4.73	68.08 ± 4.79
	(62.90 to 91.00)	(38.80 to 80.00)
2D:4D ratio	0.984 ± 0.036	0.992 ± 0.037
2D:4D normalised index[a]	1.000 ± 0.032	0.983 ± 0.033
2D:4D normalised index[b]	0.996 ± 0.032	0.985 ± 0.034
2D:4D normalised index[c]	2.775 ± 0.090	2.730 ± 0.091
Adjusted 2^{nd} finger length, mm[a]	70.67 ± 2.28	69.49 ± 2.32
Adjusted 2^{nd} finger length, mm[b]	70.64 ± 2.36	69.51 ± 2.24

Values are expressed as mean ± SD, with range in parentheses. [a]: 2-parameter power function with normal, homoscedastic error; [b]: straight line with intercept and normal, homoscedastic error; [c]: power function ratio. The normalised indices [a,b] were derived directly from the model residuals [12] in raw arithmetic space, with the 2D:4D ratio or 2D as the dependent variable and 4D and Sex as predictors. Each participant's residual was added to the predicted mean ratio for each sex at the mean 4D length in the whole sample, to obtain an adjusted 2D:4D 'ratio' or 2D free from the influence of 4D length. The normalised index [c] was directly derived from the ratio of 2D to 4D raised to the power of 0.80 and 0.76 in the right and left hand, respectively.

Table 2. Statistical models fitted to untransformed data for scaling 2D (mm) to 4D (mm) in the right hand

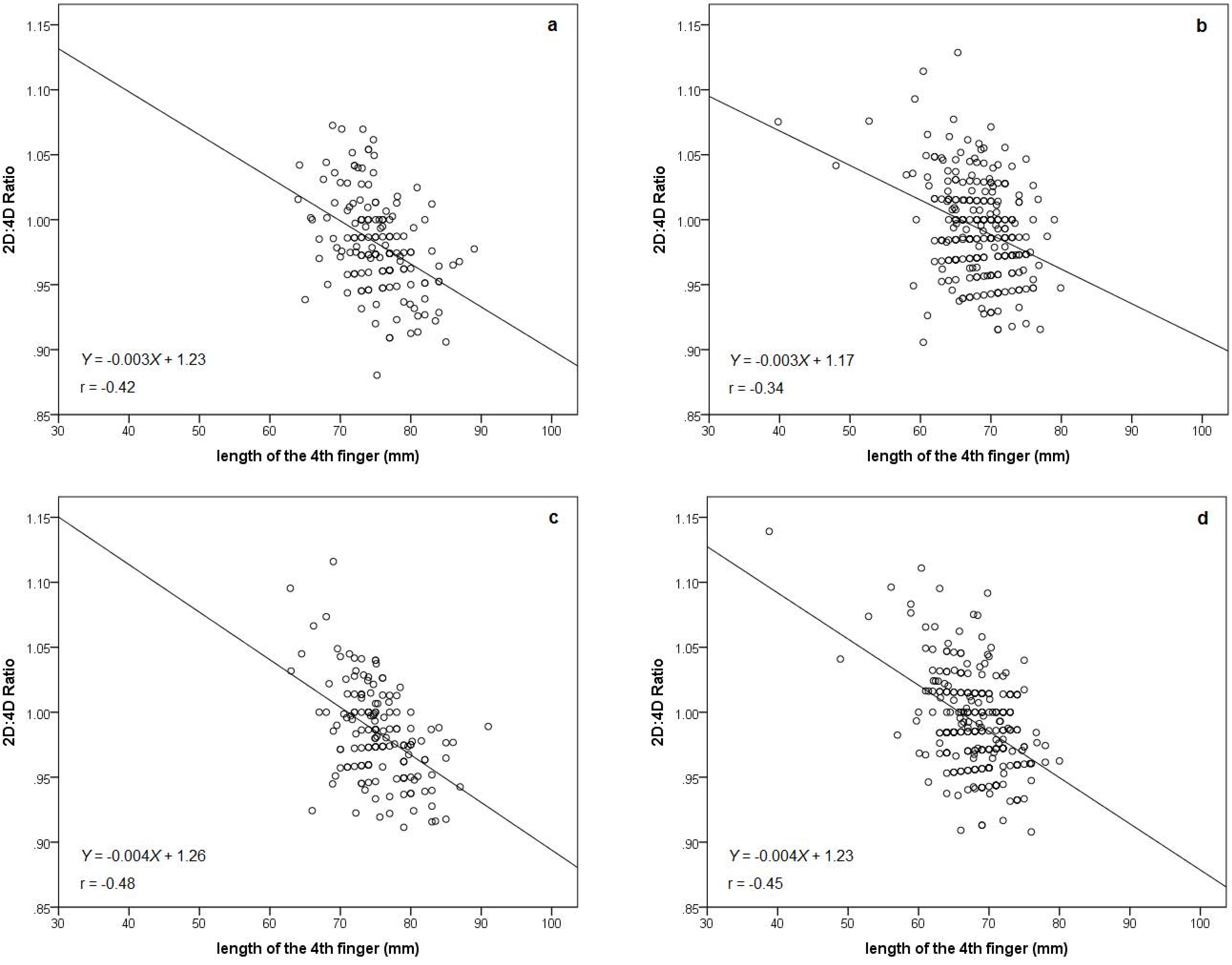
Model	AIC	ΔAIC	Inference
Straight line, no intercept, with lognormal heteroscedastic error	1984.1	61.0	no empirical support
Straight line, no intercept, with normal, heteroscedastic error Failed to converge. Convergence criterion changed to 0.011	1983.7	60.6	no empirical support
Straight line, no intercept, with normal, homoscedastic error	1979.9	56.8	no empirical support
3-parameter power function with normal, heteroscedastic error Failed to converge. Convergence criterion changed to 0.014	1929.0	5.9	plausible alternative
2-parameter power function with normal, heteroscedastic error Failed to converge. Convergence criterion changed to 0.013	1928.8	5.7	plausible alternative
Straight line, intercept, with lognormal heteroscedastic error	1928.1	5.1	plausible alternative
Straight line, intercept, with normal, heteroscedastic error Failed to converge. Convergence criterion changed to 0.01	1927.3	4.3	plausible alternative
3-parameter power function with lognormal, heteroscedastic error Failed to converge. Equation rearranged and converged	1926.5	3.5	plausible alternative
2-parameter power function with lognormal, heteroscedastic error	1925.9	2.8	plausible alternative
Straight line, intercept, with normal, homoscedastic error	1924.6	1.6	essentially equivalent
3-parameter power function with normal, homoscedastic error Failed to converge. Equation rearranged and converged	1923.8	0.8	essentially equivalent
2-parameter power function with normal, homoscedastic error	1923.1	0	Best

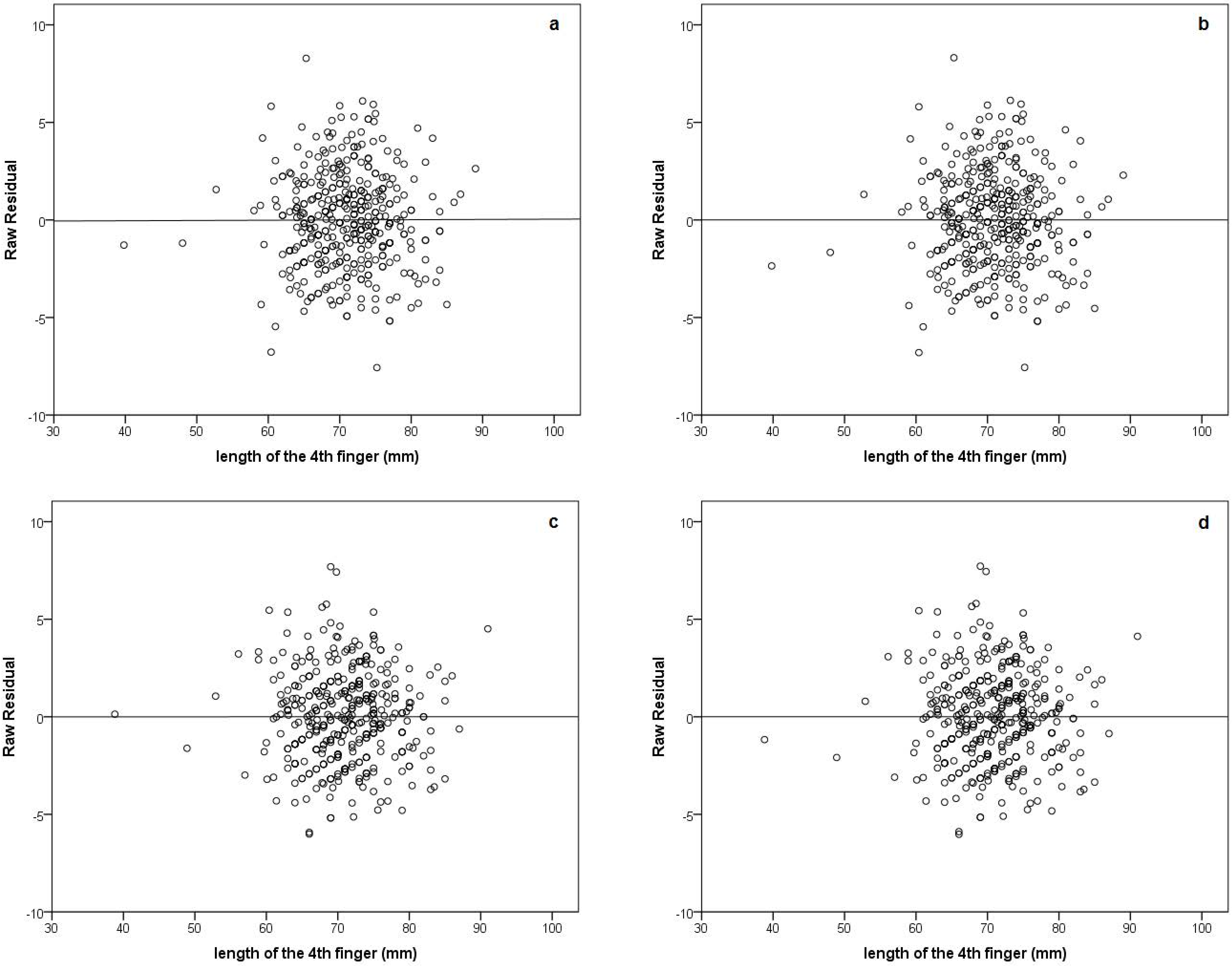
AIC = Akaike's information criterion; ΔAIC = Akaike difference

Table 3. Statistical models fitted to untransformed data for scaling 2D (mm) to 4D (mm) in the left hand

Model	AIC	ΔAIC	Inference
Straight line, no intercept, with lognormal heteroscedastic error	1978.0	103.8	no empirical support
Straight line, no intercept, with normal, heteroscedastic error Failed to converge. Convergence criterion changed to 0.013	1971.1	96.9	no empirical support
Straight line, no intercept, with normal, homoscedastic error	1962.3	88.1	no empirical support
3-parameter power function with normal, heteroscedastic error Failed to converge. Convergence criterion changed to 0.014	1882.0	7.8	weak support
3-parameter power function with lognormal, heteroscedastic error	1880.8	6.6	plausible alternative
2-parameter power function with normal, heteroscedastic error Failed to converge. Equation rearranged and converged	1880.5	6.3	plausible alternative
Straight line, intercept, with lognormal heteroscedastic error	1879.1	4.9	plausible alternative
2-parameter power function with lognormal, heteroscedastic error	1878.8	4.6	plausible alternative
Straight line, intercept, with normal, heteroscedastic error Failed to converge. Convergence criterion changed to 0.014	1877.8	3.6	plausible alternative
3-parameter power function with normal, homoscedastic error Failed to converge. Equation rearranged and converged	1876.3	2.1	plausible alternative
2-parameter power function with normal, homoscedastic error	1874.3	0.1	essentially equivalent
Straight line, intercept, with normal, homoscedastic error	1874.2	0	Best

AIC = Akaike's information criterion; ΔAIC = Akaike difference


a
2D:4D Ratio
length of the 4th finger (mm)
Y = -0.003X + 1.23
r = -0.42
b
2D:4D Ratio
length of the 4th finger (mm)
Y = -0.003X + 1.17
r = -0.34
c
2D:4D Ratio
length of the 4th finger (mm)
Y = -0.004X + 1.26
r = -0.48
d
2D:4D Ratio
length of the 4th finger (mm)
Y = -0.004X + 1.23
r = -0.45


a
b
c
d
Raw Residual
10
5
0
-5
-10
30
40
50
60
70
80
90
100
length of the 4th finger (mm)