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ABSTRACT

Evidence for a ‘Midlife Crisis’ in Great Apes Consistent with the U-Shape in Human Well-Being*

Recently, economists and behavioral scientists have studied the pattern of human well-being over the lifespan. In dozens of countries, and for a large range of well-being measures, including happiness and mental health, well-being is high in youth, falls to a nadir in midlife, and rises again in old age. The reasons for this U-shape are still unclear. Present theories emphasize sociological and economic forces. In this study we show that a similar U-shape exists in 508 great apes (two samples of chimpanzees and one sample of orangutans) whose well-being was assessed by keepers familiar with the individual apes. This U-shaped pattern or ‘midlife crisis’ emerges with or without use of parametric methods. Our results imply that human well-being’s curved shape is not uniquely human and that, while it may be partly explained by aspects of human life and society, its origins may lie partly in the biology we share with closely related great apes. These findings have implications across scientific and social-scientific disciplines and potentially in identifying ways to enhance the well-being of humans and apes.

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Keywords: aging, primate, satisfaction, evolution, affect

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Introduction

There is accumulating evidence, based on biomarker, spatial, genetic, and brain-science data, for the objective validity of subjective measures of human well-being (1-6). Published results showing a U-shaped relationship between well-being and age, with the lowest point approximately in midlife, can be traced back at least two decades to research on job satisfaction and mental health (7-9). Although some scholars have raised doubts about the existence of the shape (10-12), a large new literature indicates that human happiness follows a U-shape throughout life (13-17), except in the years right before death (15). There is corroborating evidence. After adjustment for covariates, suicide risk (18) and antidepressant consumption (19) exhibit a midlife peak. U-shaped well-being patterns have been found in over 50 nations (15, 20), including poorer developing nations. Sample sizes vary from a few hundred to millions of participants. One of the most important findings in this literature is that, as shown, for example, by Stone et al. (14) in their Figure 1, the U-shape is virtually unaffected by statistical adjustment for a large range of economic and demographic characteristics. This striking discovery seems to suggest that some of the causes of the U-shape must go beyond standard socioeconomic forces.

Also of note, the midlife dip cannot be explained by the effects of having young children in the household, and it is similar in males and females, so is not likely connected to menopausal changes or to societal gender roles (14, 15). A selection explanation, due to the greater longevity of happy people, is likewise unable to account for the midlife dip (15). One socioeconomic theory (13) is that the U-shape reflects hedonic adaptation in which impossible aspirations are first painfully felt and then, around midlife, slowly and beneficially given up. Another theory (17) is that the curve is linked to financial hardship and thus likely to be less pronounced in those older individuals with higher resources. A third theory is that human aging may bring with it the ability to experience less regret (21). In short, there is little convergence of explanations about the U-shape's origins.

We explore an alternative explanation. From a very different research tradition, work on great ape (mostly chimpanzee) development has identified similarities to humans in the development of psychological domains other than well-being (22). Thus, it is worth considering a heretofore untested theory, namely that the U-shape found in human studies of age and well-being evolved in the common ancestors of humans and nonhuman primates, particularly the great apes. If one could establish that the U-shape in well-being exists in nonhuman primates, the implications would be wide-ranging. This finding would also recommend new hypotheses for well-being researchers.

Results

In the sample of 155 chimpanzees from Japanese zoos, research centers, and a sanctuary (Sample A), the sample of 181 chimpanzees housed in U.S. and Australian zoos (Sample B), and the sample of 172 orangutans housed in U.S., Canadian, Australian, and Singaporean zoos (Sample C), multiple regression analyses indicated that linear and quadratic age effects were negative and positive, respectively (Table 1). In other words, all three samples exhibited a U-shape (Figure 1). The age-related effects were individually significant in sample A, but not samples B or C. The curves' minima were reached at, respectively, ages 28.3, 27.2, and 35.4, and were thus comparable to human well-being minima, which range from approximately 45 to 50 years. In the fourth regression, for the total sample, significant linear and quadratic age effects indicated a U-shape and were significant. Linear and quadratic age effects did not significantly differ across the samples (Table 1). Finally, the fifth regression was identical to the prior two regressions except that it did not include interaction terms. The linear and quadratic age effects again described a U-shaped function

(Figure 1) and were significant (Table 1). The curve's minimum was at age 31.9. Using 10 banded age variables revealed the same results (see Supplementary Materials).

Discussion

Although great apes have a close phylogenetic relationship to humans (23) and share many characteristics, including cultures and tool use (24, 25), the research literature on human well-being, dating back to the Second World War (13) and currently used by governments to design economic policy (20), eschewed studies of nonhuman animals. That neglect has encouraged strictly human-centered and socioeconomic explanations for patterns found by demographers, economists, psychologists, and others.

Here we used data on other primates to suggest the value of a cross-species approach in understanding human well-being. It is important to note that our findings do not rule out the possibility that species-specific forces contribute to the well-being U-shape in humans. However, they suggest that a persuasive explanation for the human U-shape needs to also account for the similarity of this trend in our evolutionary cousins, the great apes.

There are several overlapping mechanisms that may explain the well-being U-shape. One possibility is that these age differences reflect the fact that happiness is associated with longevity in humans (26) and at least one great ape species (27). Therefore, higher rates of mortality for the least happy apes, especially in later life could account for part of the higher well-being in the older ape populations. A second possibility is that the U-shape arises in humans, chimpanzee, and orangutans via similar age-related changes in brain areas (2) associated with well-being. Finally, older adults in all three species rely on behavioral mechanisms to regulate their emotions (28). For example, they may seek out situations and group members that elicit more positive emotions or shift to goals that are more attainable in older age. It is also important to consider evolutionary explanations. For example, as well-being is associated with life satisfaction, there may have been selection for individuals who have higher well-being in youth and old adulthood. These individuals, being satisfied at stages of their life where they have fewer resources to improve their lot, would be less likely to encounter situations that could be harmful to them or their kin.

Future focus should be directed towards aspects of human lives and neurodevelopment shared with other great apes. Longitudinal studies of humans and other primates examining changes in the predictors of well-being across the lifespan could help explain the mechanisms underlying the U-shaped function. Moreover, studies of age and well-being in other species of great apes and those examining the possible fitness consequences of high midlife well-being in chimpanzees, orangutans, and humans would lead to a greater understanding of its evolutionary bases. These and other comparative, evolutionary approaches offer applications beyond the midlife nadir in happiness and could affirm Darwin's (29) view that "He who understands baboon would do more towards metaphysics than Locke."

Materials and Methods

Subjects

We used three existing samples of great apes (22, 27, 30), each of which included individuals ranging from infancy to old adulthood. Sample A comprised 64 male and 91 female chimpanzees (*Pan troglodytes*) housed in 9 zoos, 1 sanctuary, and 2 research centers, all located in Japan. Age ranged from 0.2 to 51.7 years (mean = 22.3 ± 10.6 s.d.). Sample B comprised 69 male and 112 female chimpanzees housed in 14 U.S. zoos and 1 Australian zoo. Ages for 3 subjects were estimated based on the date other subjects in their zoo were rated on well-being. Ages of a further 32 subjects were imputed via regression based on the age at which they were rated on personality (correlated $r > .99$ with age at which well-being was rated).[1] Age ranged from 0.4 to 56.0 years (mean = 17.9 ± 12.5 s.d.). Sample C comprised 69 male and 103 female orangutans (*Pongo spp.*), of which 89 were Sumatran (*Pongo abelii*), 53 were Bornean (*Pongo pygmaeus*), and 30 were hybrids. These subjects were housed in 35 U.S., 2 Canadian, 1 Australian, and 1 Singaporean zoo. Ages for 8 subjects were imputed via regression based on the age at which they were rated on personality (correlated $r > .99$ with age at which well-being was rated). Age ranged from 1.8 to 51.2 years (mean = 21.2 ± 11.7 s.d.).

Measure

Well-being was assessed using a four item questionnaire based on human subjective well-being measures, but modified for use in nonhuman primates (31, 32). Item 1 asked raters to assess the degree to which a subject was in a positive versus negative mood. Item 2 asked raters to assess how much pleasure the subject derives from social situations. Item 3 asked raters to assess how successful the subject is in achieving its goals. Item 4 asked raters to indicate how happy they would be if they were the subject for a week. This questionnaire is a well-established method for assessing positive affect in captive nonhuman primates. This is based on previous studies showing that ratings on this questionnaire are consistent across raters and define a single dimension (30, 31, 33). Also, like human subjective well-being questionnaires (6, 26, 34, 35), scores on the present questionnaire are stable over time (31), associated with analogous personality traits (30, 31, 33), and both heritable and genetically correlated with personality (36, 37). Also, a study in orangutans (27) indicated that, like human well-being (26), higher scores on this well-being scale were associated with longer a lifespan.

[1] Omitting subjects whose age was imputed did not alter results.

The raters were zoo keepers, volunteers, researchers, and caretakers who knew the subjects, usually for at least 2 years (27, 30, 33). Ratings on the four items were made on 7-point scales. For samples A and C, raters were asked to indicate where on the 7-point scale a particular subject fell on a particular item. Sample B was rated using an older version of the scale that instructed raters to assign a 1 to the chimpanzee at their facility with the lowest score, a 7 to the chimpanzee at their facility with the highest score, and to freely assign values ranging from 2 to 6 to the remaining chimpanzees. Well-being in all three samples was computed by taking the mean of each item across raters and then obtaining the mean of these four mean scores. The interrater reliabilities of the individual items for each sample ranged from fair to excellent; the interrater reliability of well-being in all three samples was high (see Supplementary Materials).

Well-being scores were converted into *T*-scores for all further analyses (mean = 50 ± 10 s.d.). Means and standard deviations for the samples were: A (48.1 ± 8.8), B (47.0 ± 10.9), and C (54.9 ± 8.1). In a preliminary analysis we tested whether the instructions given to Samples A and C on the one hand and Sample B on the other influenced the linear or quadratic age effects. The interaction of instruction type and linear age effects was not significant ($b = 0.261$, $t = 1.005$, $P = 0.315$). The interaction of instruction type and quadratic age effect was also not significant ($b = -0.003$, $t = -0.638$, $P = 0.524$). Thus, there was no evidence that the association between the age effects and well-being varied as a function of instruction type.

Analyses

Researchers on human well-being typically use multiple regression, and age effects are examined after adjusting for several variables, including income, education, marital status, gender, and location. In at least one dataset the U-shape was found not to exist until adjustment for these covariates (15, 38). For our analyses we also examined associations between age and well-being using multiple regressions (39). However, our analysis of ape well-being was more conservative; we only adjusted for sex and the sample used. To avoid the multiple-comparisons problem, we focused on the single hypothesis of a quadratic relationship between well-being and age. Throughout, significance tests were two-tailed and alpha was 0.05.

In the first three regressions we tested for the U-shape in each sample separately. In each, well-being was predicted by sex (male = 1, female = -1), linear age effects (age in years), and quadratic age effects (age in years squared). In the fourth regression we combined the samples to test whether they described the same linear and quadratic age effects. Predictors in this regression included sex and two effects coded variables that tested for deviations of Sample A or B from the well-being grand mean. These effects adjusted for differences arising from Sample A being rated in Japanese by Japanese raters or Sample C being orangutans instead of chimpanzees. The regression also included variables indicating linear and quadratic age effects, and interaction terms to test whether these age effects differed across samples. The fifth regression was similar to the prior two regressions except that it did not include interaction terms.

Finally, we conducted a supplementary analysis to assess the robustness of the multiple regression analyses described above. The supplementary analysis examined the appropriateness of fitting a quadratic function to the full ape data set by checking that we did not overfit these data. To do this, we estimated the effects of age on well-being equation without imposing any parameterized structure or polynomial function. Instead, we estimated the effects of age on well-being using 10 banded age variables.

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Figure 1. The U-shape in three samples of great apes.

Well-being scores, collapsed across sex, fitted to a quadratic function for the three samples, both separately (Upper Left, Upper Right, Lower Left), and combined (Lower Right). Fitted scores were rescaled (mean = 50 ± 10 SD).

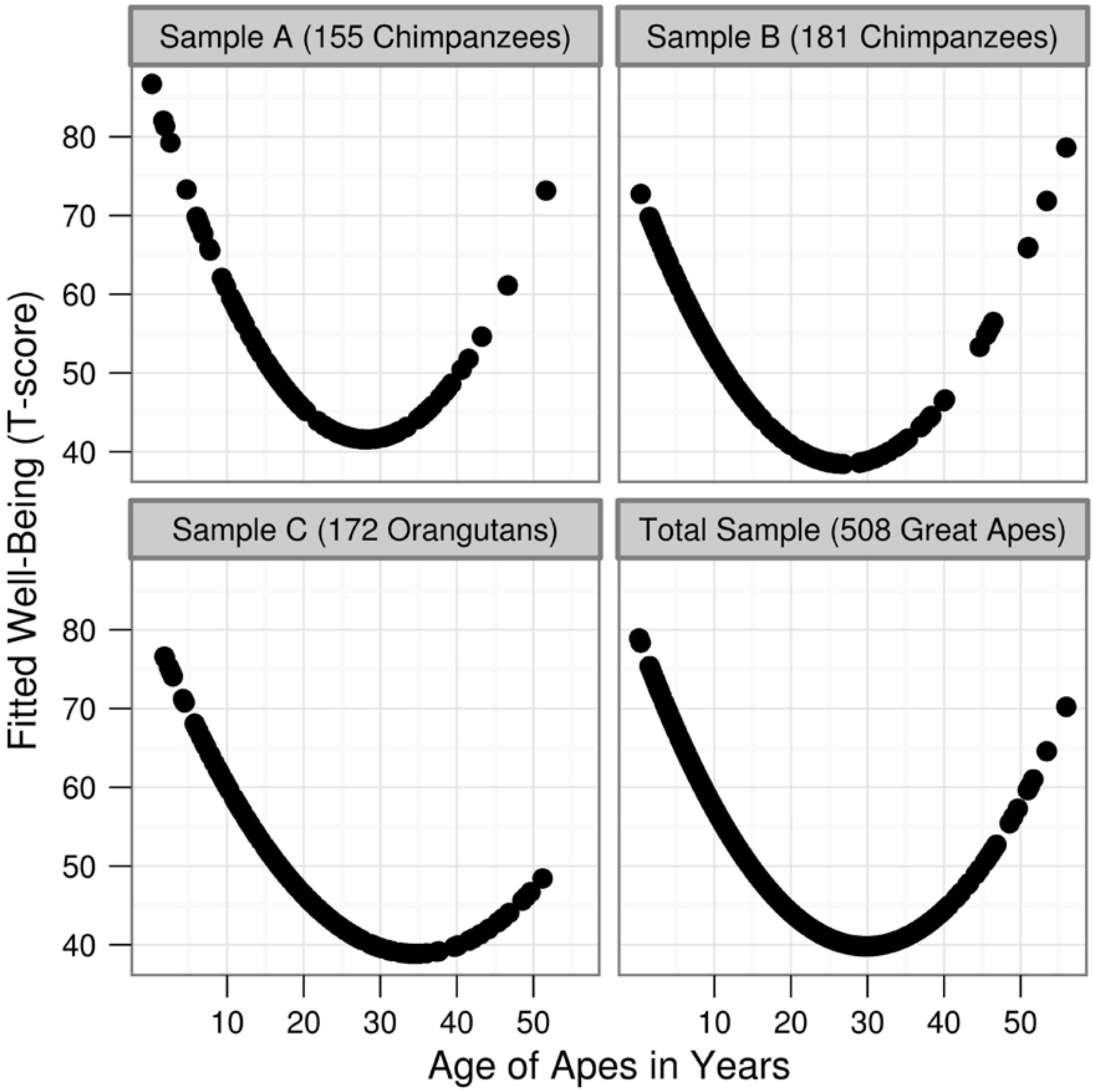

Table 1. Regression equations for chimpanzee and orangutan well-being

	b	*SE*	*t*	*P*
Sample A (n = 155)				
Intercept	56.805	2.704	21.005	< 0.001
Male	1.498	0.709	2.112	0.036
Age	-0.735	0.253	-2.910	0.004
Age^2	0.013	0.005	2.419	0.017
Sample B (n = 181)				
Intercept	50.557	2.094	24.147	< 0.001
Male	0.477	0.833	0.572	0.568
Age	-0.381	0.216	-1.768	0.079
Age^2	0.007	0.004	1.573	0.117
Sample C (n = 172)				
Intercept	59.808	2.093	28.573	< 0.001
Male	1.992	0.606	3.287	0.001
Age	-0.354	0.192	-1.841	0.067
Age^2	0.005	0.004	1.348	0.179
Total Sample (n = 508)				
Intercept	55.764	1.400	39.835	< 0.001
Sample A	0.921	2.180	0.423	0.673
Sample B	-5.132	1.732	-2.963	0.003
Male	1.301	0.421	3.091	0.002

Age	-0.491	0.132	-3.714	0.000
Age^2	0.008	0.003	3.065	0.002
Sample A*Age	-0.232	0.205	-1.134	0.258
Sample B*Age	0.118	0.169	0.696	0.487
Sample A*Age^2	0.004	0.004	1.015	0.311
Sample B*Age^2	-0.001	0.004	-0.395	0.693
Total Sample (n = 508)				
Intercept	55.215	1.316	41.962	< 0.001
Sample A	-1.502	0.598	-2.51	0.012
Sample B	-3.514	0.582	-6.037	< 0.001
Male	1.260	0.418	3.017	0.003
Age	-0.447	0.125	-3.574	< 0.001
Age^2	0.007	0.003	2.920	0.004

b coefficients for “Sample A”, and “Sample B” indicates the deviation of these groups’ well-being from the unweighted grand mean of well-being.

Supplementary Materials

The first part of this section describes the inter-rater reliabilities of the mean scores across raters of the individual well-being items and the composite well-being score in each sample. Inter-rater reliabilities estimates were defined as intraclass correlation formula *ICC*(3,*k*), which is defined as the proportion of the variance between subjects that is true score variance (40). The estimates were derived from all subjects in each sample that were rated by more than one individual. We used standard guidelines (41) to interpret the reliability of ratings. None of the items in our three samples had poor reliability (*ICC*[3,*k*] < .4) and, in all but one instance (the reliability of asking how successful an orangutan was in achieving its goals was fair), the reliabilities were good (*ICC*[3,*k*] = .60 to .74) or excellent (*ICC*[3,*k*] > .74). The reliabilities of the well-being composites were high (Table S1).

The second part of this section is included as a general robustness check. It examines the appropriateness of fitting the shape discussed in the human well-being literature, namely, a quadratic, to the full ape data set. To do this check, the analysis presented in Table S2 estimates a well-being equation without imposing any parameterized structure or polynomial function. The results reveal that, even with an elementary set of 11 banded dummy variables, the low point is reached between age 30 and age 35, and that, although sub-sample sizes are inevitably too small within each age band to allow precision on individual coefficients or a perfect non-parametric U, there is evidence broadly consistent with the study's parameterized approach.

Table S1. Inter-rater reliabilities for well-being items and the well-being composite in samples A, B, and C

	Sample		
	A	B	C
Descriptive statistics			
$n_{subjects}$	155	176	149
n_{raters}	51	71	100
$n_{ratings}$	483	610	392
maximum number of raters	5	7	6
mean ± s.d. raters per subject	3.12 ± 0.57	3.47 ± 1.45	2.63 ± 1.03
ICC(3,*k*)			
Item 1: Moods	0.76	0.75	0.71
Item 2: Social	0.72	0.79	0.72
Item 3: Goals	0.74	0.81	0.50
Item 4: Be subject	0.74	0.68	0.65
Well-being	0.81	0.83	0.73

In this table $n_{subjects}$ indicates the number of subjects used in the analyses, n_{raters} indicates the number of raters used in the analyses, and $n_{ratings}$ indicates the total number of ratings in the analyses.

Table S2. Regression equation for chimpanzee and orangutan well-being with age as a banded variable

Estimate	*b*	*SE*	*t*	*P*
Intercept	56.135	1.434	39.140	< 0.001
Sample A	-1.634	0.606	-2.697	0.007
Sample B	-3.555	0.589	-6.033	< 0.001
Male	1.282	0.417	3.073	0.002
Age ≥ 5 < 10	-4.367	1.757	-2.485	0.013
Age ≥ 10 < 15	-6.234	1.783	-3.497	0.001
Age ≥ 15 < 20	-7.472	1.786	-4.183	< 0.001
Age ≥ 20 < 25	-7.728	1.807	-4.276	< 0.001
Age ≥ 25 < 30	-4.932	1.888	-2.612	0.009
Age ≥ 30 < 35	-7.850	1.922	-4.084	< 0.001
Age ≥ 35 < 40	-6.415	2.252	-2.848	0.005
Age ≥ 40 < 45	-7.701	2.772	-2.778	0.006
Age ≥ 45 < 50	-5.474	3.006	-1.821	0.069
Age ≥ 50	-5.426	3.990	-1.360	0.174

Here $n = 508$. The *b* coefficients for "Male", "Sample A", and "Sample B" indicate the deviation of well-being of these groups from the unweighted grand mean of well-being. The *b* coefficients for each age group refer to effects of a dummy-coded variable, equal to 1 if the subject is within that age band and 0 if it is not. The reference category was comprised of individuals aged less than 5 years; the coefficient on this category is thus normalized to zero.