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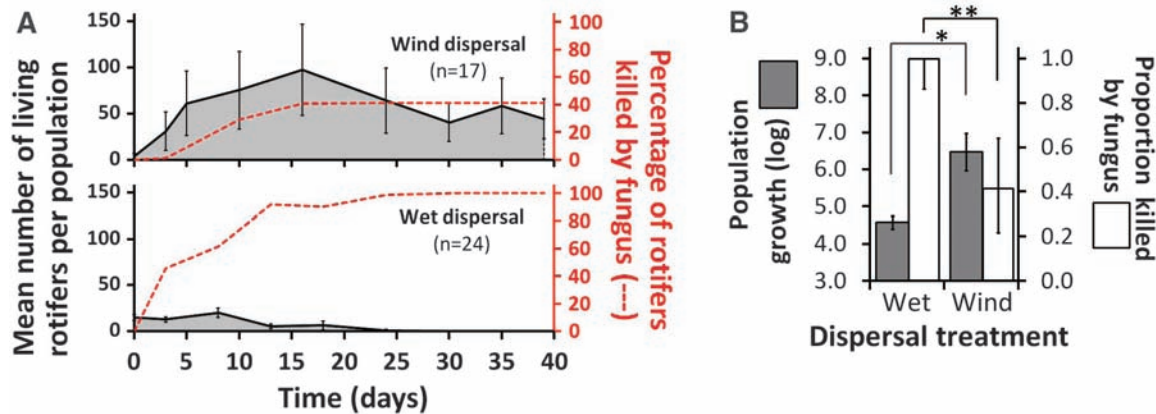
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Fig. 2. (A) Growth curves (error bars indicate $\pm 95\%$ CI) and mortality for 17 *H. elusa* populations founded by artificial wind dispersal of substrate ($5.01 \text{ mg} \pm 2.52 \text{ SD}$) from an infected source culture desiccated for 7 days. Parasites exterminated 7 populations, but 10 remained uninfected (58.8%), compared with complete mortality of all 24 control populations founded concurrently by wet transfer of 5 mg of the same infected source material. **(B)** Statistical summary of differences in (A) [see Fig. 1C legend]; * $P < 0.0001$, unpaired t test; ** $P < 0.0001$, Fisher's exact test.



to specific life stages (e.g., seeds, larvae, eggs) (15). Only bdelloid rotifers and certain tardigrades and nematodes can tolerate repeated bouts of desiccation at any life stage (14, 15), and, of these, only the rotifers occur frequently in samples of rain and wind (16). With their smaller, more aerodynamic tuns, bdelloids can colonize tiny, isolated microhabitats more rapidly than tardigrades and nematodes (17).

The Bdelloidea have been called an “evolutionary scandal” (2), because their ancient asexuality seemed to challenge all hypotheses for the long-term maintenance of sex. However, if anhydrobiotic dispersal enables bdelloid species to escape temporally and spatially from some or many natural enemies, their coevolutionary burden would be substantially reduced. Therefore, our results are consistent with a scenario in which bdelloids have evaded parasites and pathogens over evolutionary time, without incurring the costs of sexuality, by playing a never-ending game of “hide-and-seek” (11, 12). Decoupling from coevolving enemies could help to explain the ancient asexuality of the Bdelloidea under the broad array of models that derive from or incorporate Red Queen dynamics.

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Objective Confirmation of Subjective Measures of Human Well-Being: Evidence from the U.S.A.

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A huge research literature, across the behavioral and social sciences, uses information on individuals' subjective well-being. These are responses to questions—asked by survey interviewers or medical personnel—such as, “How happy do you feel on a scale from 1 to 4?” Yet there is little scientific evidence that such data are meaningful. This study examines a 2005–2008 Behavioral Risk Factor Surveillance System random sample of 1.3 million U.S. citizens. Life satisfaction in each U.S. state is measured. Across America, people's answers trace out the same pattern of quality of life as previously estimated, from solely nonsubjective data, in one branch of economics (so-called “compensating differentials” neoclassical theory, originally from Adam Smith). There is a state-by-state match ($r = 0.6$, $P < 0.001$) between subjective and objective well-being. This result has some potential to help to unify disciplines.

The concept of human well-being is important but difficult to study empirically. One approach is to listen to what human beings say. Research across the fields of psychology, decision science, medical science, economics, and other social sciences draws upon questionnaire data on people's subjective well-being (1–13). These are numerical scores (e.g., from very satisfied to very dissatisfied) in response to survey

questions such as: How happy are you with your life? Sample sizes in these statistical analyses typically vary from a few dozen individuals in a

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laboratory to many tens of thousands of people in a household survey (2, 4).

If reported well-being numbers provide accurate information about human experience—so are not merely random, deliberately or accidentally untruthful, or irredeemably affected by the possibility that they may not be comparable from one person to another—such data offer important intellectual opportunities to research scientists and practical ones to policy-makers. However, at present, there is little empirical evidence, of the sort able to convince a skeptic, that they do. Perhaps the closest to a validation (of the believability) of subjective well-being scores is the finding that there are correlations between reported happiness and blood pressure, and among emotions, relative reward, and the brain (14–18). This argument, although suggestive, faces a difficulty. The demonstration of a statistical link between physiological measures and subjective well-being answers usefully establishes that the latter are not random numbers. But skeptics can reasonably argue that it does little more than that. Biological indicators are not themselves unambiguous measures of human happiness or unhappiness.

This study focuses not on people but on places (19). Places have characteristics that human beings find objectively pleasant (Hawaiian sunshine or Colorado scenery) and unpleasant (Connecticut land prices or New York City traffic fumes); many are cardinally measurable. The study blends new data from the U.S. Behavioral Risk Factor Surveillance System (BRFSS) (20, 21), elements of the economist's compensating-differentials theory (22–24), and recent research on so-called amenity effects in happiness regression equations (25, 26). The jargon terms “compensating” and “amenity” here capture the following idea. In a country where people can live wherever they please, a place with a harsh environment—think of commuters in Anchorage at 5:30 a.m. in February—has to offer its inhabitants some offsetting feature, often an income advantage, to persuade them to stay there rather than leave to live in a different region. Similarly, intrinsically pleasant environments have to offer less, other things being equal.

The study examines life satisfaction among a recent random sample of 1.3 million U.S. inhabitants. The size of the data set, gathered between 2005 and 2008, provides opportunities denied to previous investigators. The often-used General Social Survey, for example, samples only ~3000 Americans biannually; it is too small to allow state-by-state analysis.

The BRFSS can be downloaded at www.cdc.gov/BRFSS and is a state-based system of health surveys that gathers (daily) information on health risk behaviors and disease prevalence in America. For many states, it is the only source of up-to-date data. The survey was started in 1984 by the Centers for Disease Control and Prevention (CDC). The data are collected in all 50 states, the District of Columbia, Puerto Rico, the U.S. Virgin Islands, and Guam. The aim is to “identify

emerging health problems, establish and track health objectives, and develop and evaluate public health policies and programs.” Although initially smaller in its sample, 350,000 adults are now interviewed each year; the BRFSS has become the largest (random-digit dialing) telephone health survey in the world. Although the nature of the data set means that it is not possible to record clinical data on people, the advantage is that its samples provide representative snapshots of the self-described health of people in the United States. The supplementary online material (SOM) gives further information (19).

The exact wording of the BRFSS life-satisfaction question is, “In general, how satisfied are you with your life?” Here people are able to answer with one of the following: very satisfied, satisfied, dissatisfied, or very dissatisfied. The questionnaire is publicly available at the BRFSS Web site. Information on BRFSS individuals' life satisfaction was collected for the first time in 2005. Published research on life satisfaction using this data set is thus only beginning.

Life satisfaction in the United States can be treated in a cardinal way by assigning 1 to 4 to the four answers, where “very satisfied” is assigned a 4. The mean of life satisfaction in modern U.S. data are then 3.4 ± 0.6 (SD). Well-being answers are skewed; they are more commonly in the upper end of the possible distribution presented to an interviewee.

Building on now-standard methods used in the literature (4, 9), a life-satisfaction regression equation was estimated, using 1.3 million data points, in which a number of independent variables were included. These were (seven) banded variables for different levels of household income; variables for the survey respondent's age, age squared, and gender; five variables for different ethnic types; and variables for the person's level of education and marital status, as well as for employment status: being self-employed, retired, a student, unemployed, or a homemaker. The sample used in the study was all those respondents between the ages of 18 and 85. Also included as independent control variables were eleven “dummy” variables for the month of interview, and a set of U.S. state dummy variables (because D.C. is included, the regression sample number is 51 states). It can be seen that a dummy variable that is coded zero or unity acts as a y axis intercept shifter in a regression equation. The study used a linear Ordinary Least Squares estimator in which the four possible satisfaction values of the dependent variable were assigned the integers from a high of 4 to a low of 1, and standard errors were adjusted for clustering at the state level. Substantive findings were not altered by switching to an ordered estimator. The simpler method allows coefficients (given in the first column of Table 1, each of which measures a vertical intercept shifter in a life-satisfaction equation) to be read off as cardinal life-satisfaction points.

The key contribution here—now feasible because of the availability of BRFSS data—is

that it is possible to measure the pattern of people's feelings of well-being (their life-satisfaction scores) across the geography of the United States. It was helpful that the state-by-state dummy-variable pattern of coefficients was not very sensitive to which exact demographic and personal variables were included in the life-satisfaction regression equation.

Information about how much Americans enjoy their lives is shown in Table 1. The numbers in the first column are regression-corrected life-satisfaction patterns across space in the United States; they are state-dummy coefficients. Alabama, because it comes first alphabetically, is the base category against which other states are measured; this normalization makes no difference to the analytical conclusions.

A life-satisfaction regression equation $L = L(z)$ for individual Americans lies behind Table 1. The statistical structure of these American equations was empirically similar to those found for many industrialized nations within the existing “happiness” literature (19). It controls for (that is, includes as independent z variables) the incomes and demographic characteristics of sampled individuals. This is necessary to the design of the study's test. The test is not primarily an attempt to assess the different kinds of people who are “happy,” but rather the kinds of geographic areas.

However, there is another, and older, way to try to assess the quality of life across regions. In an elementary form, it continues to be published in magazines in the form of quality-of-life rankings. More formally, it appears in the economics regression-equation literature and uses objective data rather than subjective information. Its focus is people's overall utility (or well-being). The approach relies on the idea that people enjoy having high income and spatial amenities such as sunshine hours, but that they dislike disamenities such as traffic congestion. Regression equations are estimated in which wages, rents, and house prices are the dependent variables. The independent variables in these regression equations are measures of the amenities and disamenities of the areas of the United States. The result is then estimates of “compensating differentials” by geographical area. This allows economists to read off the implied number of dollars (positive or negative) in workers' pay packets in Los Angeles that would be required to offset the unpleasantness of, say, poor air quality, and the pleasantness of high numbers of sunshine hours. The theory of compensating differentials is attributed to the Scottish economist Adam Smith (27).

Some of the most recent and thorough research in this vein, by Stuart Gabriel and colleagues (24), was published in 2003. It used, among other attributes, objective indicators for each U.S. state, such as precipitation, temperature, wind speed, sunshine, coastal land, inland water, public land, National Parks, hazardous waste sites, environmental “greenness,” commuting time, violent crime, air

quality, student-teacher ratio, local taxes, local spending on education and highways, and cost of living. Gabriel's analysis used no subjective data. Instead, these objective data were combined in a weighted average (24), where, as explained in the SOM (19), the weights were not chosen arbitrarily but rather according to coefficient sizes taken from regional wage and price equations.

In nontechnical terms, the compensating-differentials methodology of Gabriel and earlier economists argues—indeed, assumes—that higher house prices are a revealed signal of higher quality of life, other things constant, because humans will move toward the areas they find attractive, which, in turn, drives up housing prices. A spatial equilibrium is reached when a representative citizen obtains the same total utility in each region. This total utility depends on a combination of the inherent quality of life (sunny days, clean air, and so on) plus the earned income from living in that area. This methodology allows these two to be separated conceptually. It is helpful to realize that the Gabriel *et al.* state-by-state quality-of-life ranking is not exceptional. The authors note its approximate similarity to those in earlier writings (23).

The ranking, according to the Gabriel *et al.* methodology, of the inherent quality of life across the U.S. is shown in column 3 of Table 1. The ranking is computed using data for the year 1990,

which appears to be the most recent estimate in the published economics literature. As with column 1, column 3 is not to be thought of as a representation of total utility; instead, it captures nonincome elements of human well-being.

Information on both methods of life-evaluation is provided in Table 1. The first state-dummy coefficient in column 1 of Table 1 can be interpreted as showing that corrected satisfaction-with-life on average in Alaska is 0.013 cardinal life-satisfaction points below that in the base state of Alabama; Arizona is indistinguishable from Alabama, and so on down the listed states. Satisfaction with life is lowest in New York. The particularly high-satisfaction states are Louisiana and Hawaii. In Table 1, the 95% confidence intervals correspond, in each case, to a test of the null hypothesis of zero on the coefficient; it should not be presumed that there is a statistically significant difference between each of the states within low-satisfaction and high-satisfaction groupings of states.

Although it is natural to be guided by formal survey data, it might be thought unusual that Louisiana—a state affected by Hurricane Katrina—comes so high in the state life-satisfaction league table. Various checks were done [discussed in SOM (19)]. It was found that Louisiana showed up strongly before Katrina and in a mental-health ranking done

by Mental Health America and the Office of Applied Studies of the U.S. Substance Abuse and Mental Health Services Administration, based on data from the National Survey on Drug Use and Health 2004–05. Nevertheless, it is likely that Katrina altered the composition of this state—namely, that those who left were not a random sample of the population—so some caution in interpretation is called for about this state's ranked position, and that position may repay future statistical investigation.

Differences in well-being across states are not minor. In cardinal terms, as demonstrated in the SOM (19), they correspond to up to 0.12 life-satisfaction points across U.S. states, which is similar in size to the individual cross-sectional effect on life satisfaction of marital separation or unemployment, other things being equal.

These two approaches are brought together in Fig. 1. It reveals a notable match between the fully adjusted life-satisfaction levels of Table 1 and the objectively calculated Gabriel ranking. The subjective well-being and the objective well-being measures tally. The estimated linear equation is written out in full in Fig. 1 and is approximately of equation form $y = -0.003 - 0.001x$.

The gradient in Fig. 1 is negative. This is because the Gabriel method, being a ranking of quality of life across states, uses the convention that 1 is the highest ranking of quality of life

Table 1. Two ways of measuring the quality of life in America. The BRFSS life-satisfaction equation uses coefficient dummy-variable values for each state. The compensating-differentials methodology of objective quality-of-life rank, by state, is from Gabriel *et al.* (23). Alabama is included in the data (and in Fig. 1). It

is the base category, against which the other states' coefficients are normalized. In effect, Alabama has a life-satisfaction coefficient of zero [and a ranking of 26 in (23)]. Number of observations, 1,213,992. The standard errors were adjusted for clustering at the state level. CI, confidence interval; N.A., not applicable.

State	BRFSS life-satisfaction method			Comp diff. methods	State	BRFSS life-satisfaction method		
	Coefficient	[95% CI]				Coefficient	[95% CI]	Comp diff. methods
Alaska	-0.013	[-0.018, -0.008]	23	Montana	0.001	[-0.002, 0.004]	4	
Arizona	0.001	[-0.002, 0.005]	20	Nebraska	-0.044	[-0.047, -0.041]	16	
Arkansas	-0.017	[-0.019, -0.015]	3	Nevada	-0.065	[-0.068, -0.062]	29	
California	-0.076	[-0.080, -0.072]	42	New Hampshire	-0.033	[-0.036, -0.030]	43	
Colorado	-0.027	[-0.030, -0.024]	34	New Jersey	-0.078	[-0.081, -0.075]	47	
Connecticut	-0.081	[-0.084, -0.078]	32	New Mexico	-0.029	[-0.034, -0.024]	14	
Delaware	-0.027	[-0.029, -0.025]	30	New York	-0.088	[-0.090, -0.085]	50	
District of Columbia	-0.048	[-0.051, -0.045]	N.A.	North Carolina	-0.013	[-0.015, -0.012]	17	
Florida	0.004	[0.002, 0.006]	10	North Dakota	-0.030	[-0.032, -0.027]	6	
Georgia	-0.021	[-0.023, -0.020]	36	Ohio	-0.070	[-0.071, -0.068]	33	
Hawaii	0.011	[0.004, 0.018]	38	Oklahoma	-0.026	[-0.029, -0.024]	21	
Idaho	-0.014	[-0.017, -0.011]	5	Oregon	-0.040	[-0.044, -0.037]	22	
Illinois	-0.072	[-0.074, -0.069]	48	Pennsylvania	-0.067	[-0.069, -0.065]	35	
Indiana	-0.078	[-0.080, -0.077]	44	Rhode Island	-0.068	[-0.071, -0.066]	12	
Iowa	-0.041	[-0.044, -0.038]	15	South Carolina	0.001	[0.000, 0.002]	18	
Kansas	-0.044	[-0.046, -0.041]	19	South Dakota	-0.014	[-0.017, -0.010]	2	
Kentucky	-0.045	[-0.047, -0.043]	24	Tennessee	0.003	[0.001, 0.004]	28	
Louisiana	0.033	[0.032, 0.034]	8	Texas	-0.014	[-0.018, -0.010]	25	
Maine	-0.006	[-0.009, -0.003]	9	Utah	-0.026	[-0.030, -0.023]	39	
Maryland	-0.066	[-0.069, -0.064]	45	Vermont	-0.017	[-0.020, -0.014]	13	
Massachusetts	-0.070	[-0.073, -0.068]	27	Virginia	-0.033	[-0.035, -0.031]	31	
Michigan	-0.079	[-0.081, -0.077]	49	Washington	-0.046	[-0.049, -0.042]	41	
Minnesota	-0.031	[-0.034, -0.027]	46	West Virginia	-0.044	[-0.046, -0.042]	11	
Mississippi	0.001	[0.000, 0.001]	7	Wisconsin	-0.038	[-0.040, -0.035]	37	
Missouri	-0.064	[-0.066, -0.062]	40	Wyoming	-0.013	[-0.016, -0.010]	1	

(and hence the number 50, for the state of New York, corresponds to the lowest quality-of-life area in the United States). The calculated Pearson r coefficient is 0.6. With 48 degrees of freedom, the null hypothesis of no correlation is therefore rejected at the $P < 0.001$ level (in fact, approximately $P = 0.0001$) on a two-tailed test. The r^2 is 0.36; that is, ~36% of the variance in the y axis variable is explained by the x axis variable. As shown more fully in the SOM (19) and in (20), the high-satisfaction states in Fig. 1 are not simply the high-income ones.

A correlation coefficient of 0.6 is unusual by the standards of behavioral science. It is high by the cut-offs suggested by Cohen's (28) rules-of-thumb (which argued that in human data an r value over 0.5 should be seen as a large association, and 0.3 a medium one). An $r = 0.6$ is the same degree of correlation, for example, as has been found for people's own life-satisfaction readings taken 2 weeks apart (that is, using the same well-being question, asked of the same person) (29). An $r = 0.3$ has been demonstrated for subjective well-being correlated with EEG asymmetry in the brain (15). The variable on the x axis in Fig. 1 is an ordinal rank. As would be expected, an arguably preferable Spearman rank test confirms the same relation as the Pearson test. An alternative estimation method would be multilevel modeling (30, 31). The data set is too large to allow this easily, but experiments on subsamples were done. These suggested that equivalent life-satisfaction equations emerge.

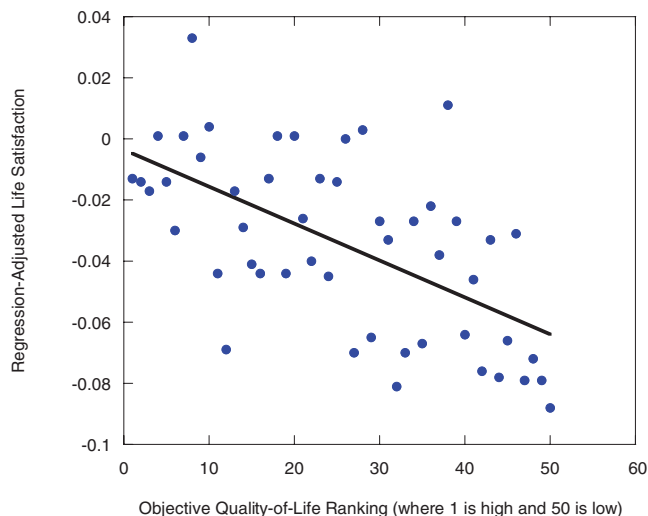
Although this study is designed as an analytical contribution, measures of subjective well-

being are becoming more widely discussed outside the laboratory. As the draft of this article was being revised, the Stiglitz-Sen-Fitoussi Commission on the Measurement of Social and Economic Progress (32), set up by Nicholas Sarkozy to assess the appropriate goals of Western governments over the remainder of the century, issued a report. Worldwide attention was garnered for its argument: "A ... unifying theme of the report ... is that the time is ripe for our measurement system to shift emphasis from measuring economic production to measuring people's well-being." "Measures of both objective and subjective well-being provide key information about people's quality of life. Statistical offices [worldwide] should incorporate questions to capture people's life evaluations, hedonic experiences and priorities in their own survey." [Executive Summary of Commission Report (32), pp. 12 and 16].

In this vein, the current study's principal contribution, Fig. 1, offers a possible bridge between different ways of thinking—between, in particular, the fields of hedonic psychology and neoclassical economics (the latter has traditionally been hostile to the use of data on subjectively reported feelings). It offers a cross-check on the spatial compensating-differentials theory of economics and regional science. It may also be relevant to the work of behavioral scientists, geographers, applied psychologists, and mental-health specialists. The study's finding suggests that subjective well-being data contain genuine information about the quality of human lives.

Fig. 1. Fitted equation: Adjusted Life Satisfaction = $-0.0035 - 0.0012$ Objective Rank; $r = 0.598$. Each dot is a state. The correlation is significant at $P < 0.001$ on a two-tailed test. This figure plots state dummy coefficients from a life-satisfaction equation against state rank in quality of life from the compensating-differentials results, based on objective amenities like sunshine hours, of Gabriel *et al.* (24). Life satisfaction is coded for each individual from a score of 4 (very satisfied) to 1 (very dissatisfied). On the y axis, the regression controls for household income, as well as the survey respondent's gender, age, age squared, education, marital status, employment status, and race, and also year dummies and month-of-interview dummies. Alabama is included. Washington, DC, is omitted from (24) and thus from here. The bottom right-hand observation is New York. Wording of the question in the BRFSS questionnaire (questionnaire line 206):

- In general, how satisfied are you with your life?
 1 Very satisfied
 2 Satisfied
 3 Dissatisfied
 4 Very dissatisfied



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Supporting Online Material

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 References

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