

Reduced functional status and social conflict increase risk of depression in adulthood among modernizing Amazonian forager-farmers

Jonathan Stieglitz^{*1}, Hillard Kaplan^{1,2}, Eric Schniter², Christopher von Rueden³, and Michael Gurven³

*Corresponding author

¹Department of Anthropology, University of New Mexico

²Economic Sciences Institute, Chapman University

³Integrative Anthropological Sciences Unit, University of California-Santa Barbara

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Abstract

This paper presents and tests a novel evolutionary framework regarding mood variation, in the continuum from well-being to depression, among Tsimane forager-farmers of Bolivia. Pre-modern societies are under-represented in studies of well-being, and research into factors affecting well-being in those societies may provide new insights into evolutionary bases of mood disorder. We propose that significant mood variation exists in pre-modern societies, and that mood responds to two fitness-related features of life: 1) economic productivity as it is affected by functional status and health; and 2) social standing. As part of the Tsimane Health and Life History Project, a representative cross-section of adults \geq age 30 ($n=849$) completed a culturally-appropriate affect questionnaire. Economic, demographic and epidemiological data were collected during medical exams and census updates ($n=63$ villages). Results show a strong positive relationship between functional status and well-being, even after controlling for age, sex, multiple indicators of current physical condition, social conflict and modernization. Depression is associated with dyadic social conflict, but only conflict with non-kin. The Tsimane age profile of well-being is not characterized by a “mid-life crisis”. Rather, depression increases with age, as functional status, health and productivity decline. Modernization is marginally associated with depression, although market skills and access are associated with lower depression scores later in life. Depression appears to be a response to conditions experienced over human history, and not simply a byproduct of modern environments.

Introduction

Persistent low mood or depression¹ is an evolutionary conundrum given its prevalence and high cost. Converging lines of evidence suggest that lower well-being increases risk of cardiovascular and other morbidity, rate of disease progression and mortality in diverse populations (1). Depression is a leading cause of foregone productivity due to disability worldwide (2). Major depressive disorder is estimated to result in 27 lost workdays per ill worker per year in the US (~10% of workdays) and \$37 billion in annual human capital loss for the US labor force (0.3% of GDP) (3). Positive mood may be part of a broad complex of resilience and well-being, and understanding factors affecting variability in mood are of obvious clinical and practical importance.

Most research on depression is conducted in developed nations, and we know very little about variation in mood states in pre-modern societies. Does depression exist, and if so, what are its causes? Research in societies living under conditions more similar to the ones in which our species evolved should provide new insights into the selective pressures that shaped mood variability over human history. Extant hunter-gatherers and horticulturalists are energy-limited, have high mortality, lack significant material wealth, and lack access to public sanitation and modern healthcare. Yet they are also relatively egalitarian, physically active, have high fertility, and reside in small-scale, kin-based groups with little social isolation and frequent inter- and intra-generational resource transfers. High rates of depression in modern societies may be due to pathological features of modern environments such as rampant inequality, erosion of family ties, or intense social competition in heterogeneous groups (4). Determining whether depression is an adaptive response to more general conditions, or a byproduct of adaptive

¹Depression has clinical significance and is defined by the Diagnostic and Statistical Manual of Mental Disorders (DSM). However, when we use the term depression we refer more generally to the cluster of symptoms often associated with depression (e.g., sadness, loss of interest, fatigue, and diminished ability to concentrate).

mechanisms triggered by modern environments requires data from pre-modern societies. These data are useful to test the generalizability of alternative hypotheses and advance a more general framework for understanding susceptibility to mood disorder.

A prominent hypothesis dating back to Darwin is that mood and emotion, which have valence and vary in intensity, evolved by natural selection to motivate physiological and behavioral responses to recurring adaptive problems (5)². Positive valence motivates continuation of prior behaviors associated with its occurrence, while negative valence motivates behavioral disengagement and pursuit of alternative strategies (4). Existing adaptive explanations suggest that depression functions mainly to mitigate conflict and elicit social support. Depression is hypothesized to compel the loser of a conflict to avoid greater costs by signaling submission (6), avoid exclusion from vital social relationships (7), improve one's ability to analyze and solve social problems (8), or solicit greater investment from a social partner by imposing costs on that partner (labor strike metaphor) (9). de Catanzaro proposes that extreme, self-destructive manifestations of depression (i.e. suicide) may be more likely among individuals who are a net burden on kin (10); suicide may therefore mitigate inclusive fitness losses. Because depression is costly to the individual, some argue that depression provides an honest signal of need to potential sharing partners (8). Factors affecting variation in need may therefore co-vary with depression, although the mechanisms have not been explored in pre-modern societies.

We propose an alternative approach to understanding variation in mood states from well-being to depression that builds on Darwin's initial insights. The production and transfer of food resources to descendants is a fundamental determinant of fitness in pre-modern societies (11). Supporting the food needs of children and grandchildren appears to be a universal feature of all pre-state societies that have been studied quantitatively. Our hypothesis is that mood state will vary directly with the ability to produce and transfer resources, as determined by age, health, energetic and functional status and the ability to work. Like previous adaptive explanations, the "productivity hypothesis" links inclusive fitness outcomes to well-being, and identifies human sociality as critical to understanding variability in well-being. Unlike other explanations, the productivity hypothesis predicts that productive capacity directly affects mood independently of inter-personal relations, and that productive capacity might indirectly affect mood by influencing inter-personal relations. The productivity hypothesis suggests that the relationship between age and well-being in adulthood is mediated by productivity, and that factors affecting variation in productivity (e.g., epidemiological, demographic, economic, ontogenetic and psychological) will co-vary with well-being. The first goal of this paper is to test predictions derived from the productivity hypothesis.

In pre-modern foraging and forager-horticultural societies, food sharing and mutual aid are necessary to buffer risks associated with a variable food supply and morbidity that inhibits work. Social conflict threatens the flow of food and aid and is costly where bi-directional resource transfers across households with shared fitness interests are common. Unresolved conflict can lead to reduced transfers, theft, fighting, migration and homicide. Current adaptive explanations of depression that highlight the role of social conflict do not specify whether certain types of conflict are associated with more intense bouts of depression, or whether certain relational characteristics of conflicting dyads might affect well-being. Our second goal is to test the hypothesis that social conflict is associated with mood variation and depression, which has never been tested under pre-modern conditions using a large representative sample of adults. We also ask whether social conflict with kin or non-kin has greater effects on well-being, since conflict with kin may be the most serious but also the easiest to resolve. This analysis helps identify the context in which social competition affects well-being. All else equal, unresolved conflict with kin may entail greater fitness costs than unresolved conflict with non-kin, because kinship helps structure the direction and magnitude of resource transfers in small-scale societies. But as fitness interests converge, costs of foregone transfers and conflict-related violence generally increase, as do the benefits of reconciliation. If reconciliation is more likely to occur following conflict with kin relative to non-kin, risk of persistent depression due to kin conflict may be low relative to conflict with non-kin. For transitioning subsistence-level populations, if conflict with non-kin is associated with discrimination and systemic barriers to improving access to critical resources (e.g., land rights, healthcare), the association between unresolved conflict with non-kin and depression may be chronic.

Our final goal is to test the hypothesis that modernization (proxied by Spanish fluency and distance to the closest market town of San Borja) is associated with depression. While modernization entails greater access, on average, to money, goods, services, and schooling, shortcomings of the "more

²Moods are long-lasting emotional states that persist in the absence of triggering stimuli.

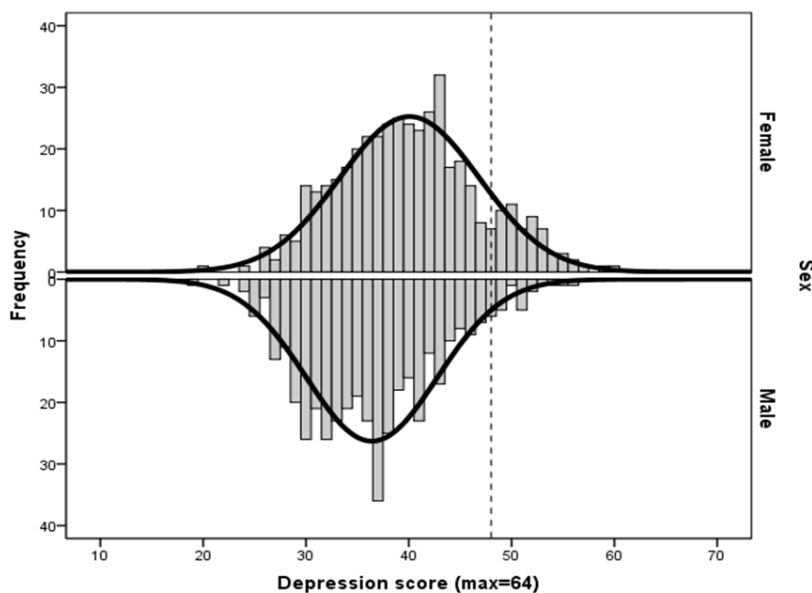
is better” approach to well-being regarding market wealth are well documented (12). Material aspirations may actually increase with education, wealth or exposure to wealthy reference groups throughout life, inevitably leading to increases in perceived shortfalls between goals and accomplishments. Moreover, if some individuals perceive themselves as unproductive relative to peers from reference groups participating in the market economy (e.g., due to relative poverty, less formal schooling or inability to speak the dominant language), they may shun market participation altogether, further violating the assumption that market wealth positively co-varies with well-being. For natural fertility populations in the early stages of demographic transition, non-market goals may be just as important to well-being as market goals, and include maintaining high levels of subsistence productivity, good health (for oneself/kin), high fertility, and strong reciprocal sharing networks. An alternative view is that well-being depends upon the discrepancy between goals and accomplishments across multiple fitness-relevant domains, where the relative importance of each domain to an individual is a facultative response (i.e. reaction norm) to variation in individual experiences or condition.

Results

Descriptives

Depression scores are normally distributed (mean±SD=38.3±6.8, range=19-60, n=849), and higher scores are more common among women (figure 1). Women score 11% higher in depression than men after controlling for age (marginal mean score±SE for women and men=40.2±0.3 and 36.3±0.3, respectively). Mean item score for women exceeds that of men for all 16 items (figure S1), and 9/16 items after adjusting for the number of tests (Bonferroni-corrected $\alpha=0.1/16$ or 0.006). For both sexes, higher depression scores are associated with older age, greater disability, reduced subsistence involvement, greater social conflict, and residential proximity to town (no controls; table S1).

Figure 1. Frequency distribution of depression scores by sex (n=429 women, 420 men). A reference line at 48 indicates number of women (15%) and men (6%) whose mean item score ≥ 3 .



Does depression increase with age, lower energy reserves, and perception of deteriorating health?

Depression scores increase with age, peaking in the late 70s and then gradually declining thereafter (figure S2; table S2: model A). We use body mass index (BMI) as a proxy of energy reserves, and find that BMI is independently associated with depression score (Std. $\beta=-0.08$, $p=0.018$, controlling for age, age^2 and sex, $n=747$) (table 1: model A). The increase in depression score with age is especially evident among those below median BMI (figure S3; table S2: model B).

Table 1. OLS regression coefficients for predictors of depression score (intercepts omitted). Betas represent change in % maximum possible score.

Predictor	MODEL A: Baseline		MODEL B: Baseline + functional status		MODEL C: Baseline + functional status + conflict		MODEL D: Baseline + functional status + conflict + modernization		
	Unstd. B	p	Unstd. B	p	Unstd. B	p	Unstd. B	p	Std. β
Age (years)	0.618	0.037	0.270	0.70	-----	-----	-----	-----	-----
Age ²	-0.004	0.100	-0.002	0.66	-----	-----	-----	-----	-----
Sex=male	-6.286	<0.001	-3.591	<0.01	-4.027	<0.01	-4.565	<0.01	-----
BMI (kg/m ²)	-0.287	0.018	-0.367	0.05	-0.284	0.11	-0.483	0.01	-0.15
Disability score ^a			1.276	<0.01	1.592	<0.01	1.503	<0.01	0.44
Subsistence involvement score ^b			-1.216	0.02	-0.621	0.18	-0.941	0.06	-0.11
Social conflict score ^c					0.924	0.07	1.304	0.02	0.14
Spanish fluency (fluent vs. none)							3.758	0.10	-----
Distance to San Borja (km)							-0.056	0.07	-0.12
Adj. R ² (N)	0.11 (747)		0.18 (290)		0.29 (244)		0.33 (197)		

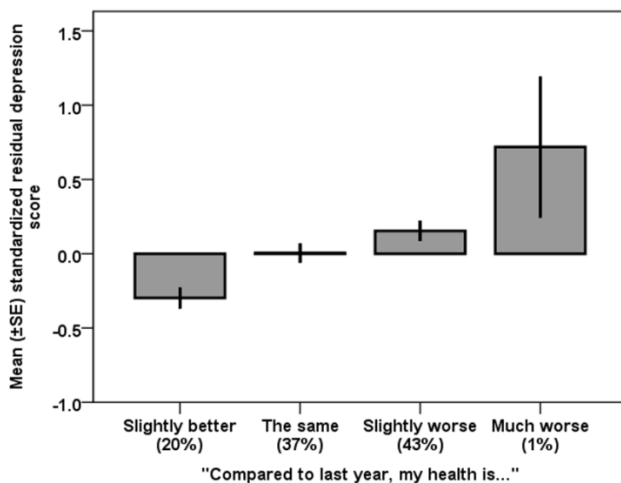
^aSum of performance difficulty for 11 mild exercises; higher scores indicate greater disability

^bSum of continued involvement in daily sex-specific tasks; higher scores indicate greater involvement

^cSum of recent conflicts reported across dyads; higher scores indicate greater conflict

Analysis of self-reported health data corroborates these results. Even after controlling for age, sex, BMI, Spanish fluency and distance to the market town of San Borja, Tsimane reporting “much worse” health compared to the prior year score 1.2 SD units higher on depression, on average, than Tsimane reporting “slightly better” health, which corresponds to a 17% increase in maximum possible score (figure 2). No Tsimane reported “much better” health compared to the prior year.

Figure 2. Perception of deteriorating health is associated with depression score after controlling for age, sex, BMI, Spanish fluency and distance to the market town of San Borja. Percentages \neq 100 due to rounding error (n=579).



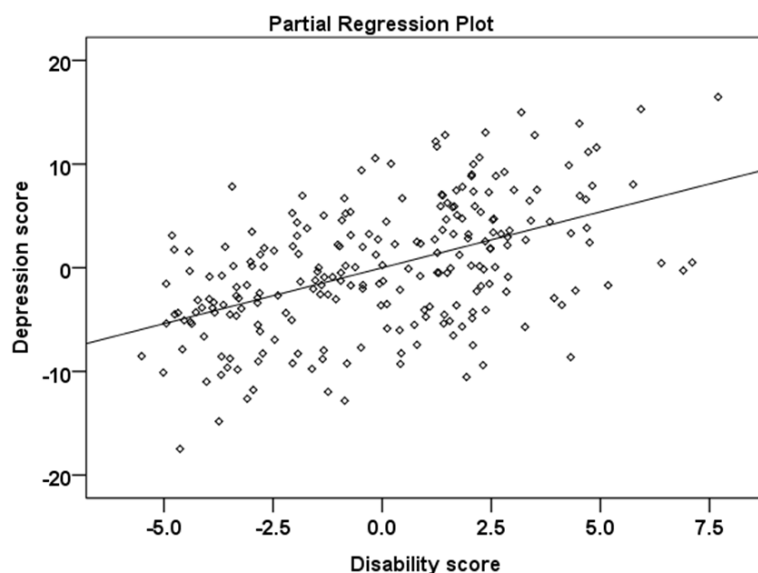
Does depression increase with greater disability and reduced subsistence involvement?

We utilize two derived measures as additional proxies of functional status: a “disability score” and a “subsistence involvement score” (see Materials and Methods). While the former may partially capture short-term reductions in functional status due to injury or acute illness, both measures also proxy longer-term functional status. Therefore, any association between depression and reduced functional status is unlikely to be solely driven by acute declines in functional status.

As might be expected, disability score increases with age: Tsimane ≥65 years score 8% higher on disability compared to their younger peers aged 40-64 ($p=0.012$, $n=352$) after controlling for sex, which has an independent effect (women score 8% higher on disability, $p=0.002$, controlling for age dummy). Subsistence involvement score also decreases with age for both sexes (not shown). Greater energy reserves mitigate age-related decline in functional status by prolonging involvement in subsistence activities: rate of decline in subsistence involvement score is greater for individuals below median BMI (interaction p -value=0.015, controlling for sex, $n=699$) (figure S4).

Disability and subsistence involvement scores are independently associated with depression score in the predicted direction after controlling for other factors (table 1:model B). Disability score mediates the effect of age on depression score, which no longer remains a significant predictor. Individuals in the top decile of disability score 16% higher on depression than individuals in the bottom decile (marginal mean score±SE for top vs. bottom deciles=42.9±1.3 vs. 37.1±1.2, controlling for sex and BMI, $n=65$). To examine whether acute illness affects the relationship between disability and depression, we control for physician diagnoses (present=1, absent=0) of common ailments including arthritis, conjunctivitis, and musculoskeletal, respiratory and gastrointestinal problems, based on clinical exams. Because co-morbidity is common, we include the sum of the diagnoses as a control. Indeed, summed diagnoses predicts depression ($p=0.027$, controlling for sex, BMI and disability score), such that each additional diagnosis corresponds to a 1.2% increase in maximum possible score. In this model, the effect of disability score on depression percentile strengthens (Unstd. B=1.69, $p<0.001$, $n=231$, adj. $R^2=0.3$) (figure 3), and disability score alone explains 25% of the variance in depression score.

Figure 3. Disability predicts depression score after controlling for sex, BMI and clinical diagnosis of common ailments at time of study ($n=231$).

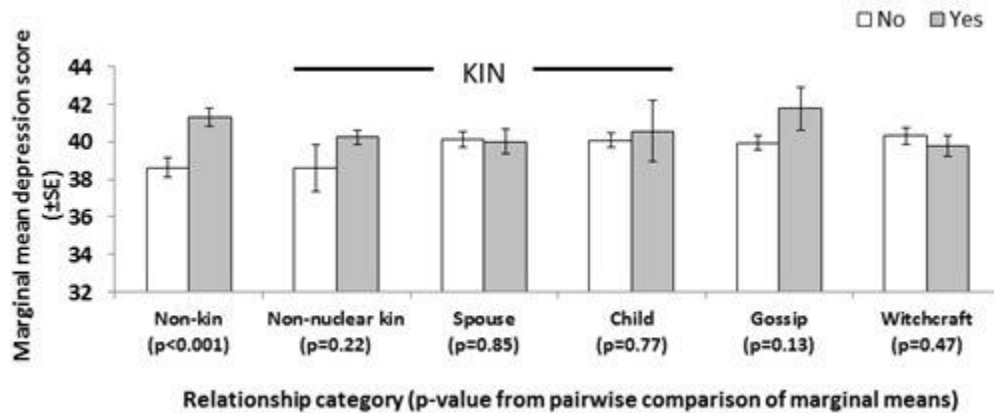


Does depression increase with social conflict?

Greater social conflict is associated with depression score after controlling for other factors (table 1:model C). Compared to those reporting no conflict, individuals scored higher on depression if reporting recent conflict among 4/6 categories of social partners (non-kin, non-nuclear kin, child, and gossipers;

same controls). However, only those reporting conflict with non-kin (generally non-Tsimane Bolivians) scored *significantly* higher on depression (increase of 7%, figure 4).

Figure 4. Depression score by whether recent conflict is reported (controlling for sex, BMI, disability score, and subsistence involvement score, n=244)



Does depression increase with modernization?

Both proxies of modernization are marginally associated with depression score in the predicted direction, and the full model explains 33% of the variance (table 1:model D). Fluent Spanish speakers score 6% higher than non-fluent speakers (same controls; marginal mean depression score \pm SE for fluent and non-fluent speakers=41.8 \pm 1.2 and 39.4 \pm 0.8, respectively, n=197). To examine whether this difference is due, in part, to differential understanding of an ordinal scale based on systematic differences in linguistic proficiency, we compared variances of item scores among fluent and non-fluent Tsimane for all 16 items (H_0 : equal variances across groups; H_A : higher variances for fluent vs. non-fluent). With Bonferroni corrections for 16 tests, a liberal adjusted p-value is 0.1/16=0.006. Using the pooled sample of men and women, only 1/16 tests satisfy this criterion (item 12: eat more/less). Therefore, any association between depression and fluency is unlikely to be solely driven by differences in the use of an ordinal scale due to differences in linguistic proficiency. The fact that distance to town is inversely associated with depression score even after controlling for fluency and other factors supports this interpretation.

As might be expected, Tsimane residing near town are significantly more likely to report conflict with non-kin (adjusted OR/10 km=1.10, p=0.009, controlling for age, n=760). Model fit is not improved by adding main effects of sex, fluency, or a fluency-by-town distance interaction term. Tsimane residing near town are not more likely to report conflict with any other relationship category (not shown).

While fluency may be associated with more frequent social comparison with wealthier and healthier non-Tsimane Bolivians, fluency also eliminates linguistic barriers to improving health by facilitating communication with medical professionals in town. Fluency also increases Tsimane men's wage opportunities by improving their ability to negotiate sales of subsistence items, and by helping men develop relationships with potential employers. We find that Spanish fluency interacts with age: well-being marginally increases (i.e. depression scores marginally decline) with age for fluent speakers (interaction p=0.10, using controls from table 1:model D) (figure S5). There is a 12% decline in maximum possible depression score from age 50 to 75 for fluent Spanish speakers, and minimal age-related change in score for Tsimane with no fluency. Distance to town interacts with age in the same direction: depression scores decline significantly with age for Tsimane residing closer to town (interaction p=0.009, same controls). There is a 5% decline in maximum possible score from age 50 to 75 for Tsimane residing closer to town; for Tsimane residing farther from town, depression score increases by 4% of the maximum over the same age range (figure S5).

To test whether modernization has different effects on well-being for men and women, we added sex-by-Spanish fluency and sex-by-town proximity interaction terms and found no significant associations. In addition, Spanish fluency does not interact with town proximity to affect depression score.

Local perceptions of how to improve quality of life

Inability to produce enough food to meet subsistence demands and sickness are the most common complaints that detract from quality of life (table 2). Social conflict also detracts from quality of life, as does the discrepancy between individual goals and accomplishments regarding market participation.

Table 2. “If you could change something in your life to make you happier, what would you change?” (free-list)

	MEN (n=349)	WOMEN (n=374)	COMBINED (n=723)
Response	% would change (rank)	% would change (rank)	% would change (rank)
Complete subsistence tasks	50 (1)	27 (2)	38 (1)
Improve own health	28 (2)	40 (1)	34 (2)
Obtain more modern goods/services	28 (2)	10 (5)	19 (3)
Reduce social conflict	9 (4)	7 (7)	8 (6)
Improve access to food	9 (4)	8 (6)	9 (5)
Live closer to natal kin	7 (6)	17 (3)	12 (4)
Improve health of descendants	4 (7)	11 (4)	8 (6)
Re-marry (if unmarried)	2 (8)	1 (8)	2 (8)
Improve health of other kin	2 (8)	1 (8)	2 (8)
Easier integration into market	1 (10)	0 (12)	<1 (11)
Greater belief in god	1 (10)	<1 (10)	1 (10)
Return to traditional lifestyle	<1 (12)	0 (12)	<1 (13)
Nothing	<1 (12)	<1 (10)	<1 (12)

Discussion

In a large representative sample of Tsimane forager-farmers we find that reduced productive capacity in adulthood is associated with depression, even after controlling for age, sex, social conflict and multiple indicators of current physical condition and modernization. Tsimane self-reports of current health relative to the prior year and their perceptions of how to improve quality of life independently support a link between productive capacity and well-being. Similarly, Iraqw and Datoga women of rural Tanzania report hunger and morbidity as major life stressors (13). Hunger and morbidity affect physical condition and one’s ability to produce and transfer resources.

In pre-modern societies, the link between functional status and well-being may be especially strong, because mitigating disability-related production deficits with modern technology (e.g., hearing aids) or by liquidating savings accounts are not viable options. Reduced productive capacity can compromise health, reduce involvement in reciprocal sharing networks, reduce reproductive opportunities, increase dependency on others (especially kin) and lower the magnitude of transfers to kin, all of which may reduce inclusive fitness.

Previous large-scale longitudinal and cross-sectional studies across diverse societies have shown a strong positive relationship between functional status and well-being (14, 15). In market societies, unemployment compromises ability to produce and transfer resources, and unemployment is a major cause of depression (16). Across diverse societies, reduced productivity can trigger depression due to increased anxieties over inability to complete tasks, poor health of oneself/kin, resource scarcity and decreased valuation by social partners. The productivity hypothesis of mood provides an ultimate explanation for the consistent finding in Western clinical samples that perceived or actual lack of control over life events elicits depressive symptoms (17).

Tsimane depression increases with age, and is not characterized by a “mid-life crisis” (figure S2), which contrasts with previous reports, mainly from industrialized societies and other great apes, of an invariant “U-shape” in well-being (18, 19). Productivity and the ability to transfer resources also decline with age. We have shown in previous papers the importance of the contributions of older Tsimane to the well-being of their descendants (11, 20). Given the importance of being productive even as grandparents,

it is perhaps not surprising that depression increases as productive capacity is lost. Our data show that aging per se is not related to depression (table 1:model B). While aging is associated with declining motor coordination, strength, endurance, sensory abilities, and productivity (20), greater somatic energy reserves later in life can partially offset age-related declines in productivity, which can affect well-being (figure S3-4).

As in industrialized societies, adult Tsimane women report lower well-being than men. Women also score higher on disability than men, and future research should examine whether the consistent sex difference in well-being across cultures is affected by functional status.

Depression is also associated with social conflict (table 1:model D), but only conflict with non-kin (figure 4). Conflict with non-kin, particularly non-Tsimane, often involves exploitative market transactions (e.g., debt peonage) and discrimination, each of which may induce stress. While unresolved conflict with both kin and non-kin may involve imbalances in exchanges of food, labor or money, the costs of prolonged conflict and retaliation are greater for kin due to shared fitness interests and kin-based residence. This suggests that relationships with kin are more resilient to conflict, more likely to result in conflict resolution, and perhaps less likely to induce low mood. Amongst kin, relatively short-term proxies of relationship quality might be less important in affecting well-being than whether a union is at risk of dissolution. Taken together, these results are consistent with multiple adaptive models of depression (e.g., facultative disengagement, social rumination, signaling submission, labor strike), and future research should prioritize testing competing model predictions.

The relationship between mood and modernization is complex and warrants further study. Spanish fluency and town proximity are positively associated with depression score (although these effects are marginally significant, see table 1:model D), despite the fact that modernization is associated with lower mortality rates among Tsimane (21, 22). Modernization may be associated with systemic discrimination by non-Tsimane, increasing awareness of the scope of inequality through social comparisons with wealthier and healthier individuals, and greater social conflict with non-kin, each of which may induce stress and depression. Modernization may also render uneducated Tsimane, particularly older cohorts with vast traditional knowledge but little Spanish fluency or market participation, especially susceptible to depression if they perceive declines in their own value to kin (all else equal). Indeed, we find that market skills and access are associated with lower depression scores later in life (figure S5), possibly because Spanish fluency and town proximity improve Tsimane access to modern healthcare. These findings are noteworthy because they indicate that modernization may be associated with depression even in the absence of significant wealth disparities characteristic of modern societies, where socioeconomic status may be a strong mediator of well-being (14, 23).

There are several limitations of this study. The study design is cross-sectional and we are unable to distinguish between shorter versus longer bouts of depression. This limits our ability to establish that loss in productive ability drives depression. However, the fact that: a) age itself is exogenous; b) disability and loss of productive capacity are age-related; and c) age effects become non-significant when disability is taken into account together provide strong suggestive evidence for a causal link between productive capacity and depression. Causality is likely to be bi-directional as well, if depression lowers productive capacity.

Given the culturally-specific nature of our instrument, assessing prevalence of mood disorder among Tsimane is not straightforward, and we are unable to make clinically significant diagnoses (e.g., depressive vs. anxiety disorder). This makes situating Tsimane results in cross-cultural context difficult at present. In a large sample of Americans aged 18+, one-month prevalence rate of major depressive disorder for men was 1.6% and for women 2.9%; of mood disorder for men was 3.5% and for women 6.6%; of dysthymia for men was 2.2% and for women 4.2%; and of anxiety disorder for men was 4.7% and for women 9.7% (24). If we assume uniform co-morbidity rates across these four disorders for both sexes and omit co-morbid cases entirely (23% of those diagnosed with at least one DSM-III disorder had a co-occurring disorder) (25), then a conservative probability of experiencing any of the four disorders for men is 9.2% and for women 18.0% (5.6% for men and 10.6% for women if we omit anxiety disorder, which is highly co-morbid with depressive disorder). Among the Tsimane, 6% of men and 15% of women regularly experience depressive symptoms (figure 1), which falls within this range and may constitute mental disorder. While cognitive and physiological effects of depressive symptoms may differ greatly across societies, depression appears to be a response to conditions experienced over human history, and not simply a byproduct of modern environments.

Materials and Methods

Study population. Tsimane (pop. ~11,000) are semi-sedentary forager-horticulturalists, inhabiting 90+ villages that vary in proximity to the closest market town of San Borja (mean±SD distance to town=42±22 km, n=70 villages). The vast majority of the Tsimane diet (>90% of calories) comes from fishing, hunting and slash-and-burn horticulture. The remainder comes from market items obtained through trade with itinerant merchants, or bought with cash earned from either men's sporadic wage labor or sale of cultigens, wood or thatched roof panels. Tsimane maintain their indigenous language, which is unrelated to Spanish, as a first language. Many villages now have schools run by bilingual Spanish-Tsimane teachers, and while Spanish is taught in school, only 11% of adults in the sample are fluent in Spanish. Schooling is not necessary to attain fluency; many older Tsimane without any schooling speak Spanish based on lifetime interactions with non-Tsimane Bolivians. While Tsimane are in the early stages of demographic transition, they maintain high fertility (total fertility rate=9) and infant mortality (13% of infants die in their first year).

Affect questionnaire. Subjective reports of health and well-being convey valid information about quality of life (26). To evaluate negative affect we developed a culturally-appropriate, 18-item questionnaire based on focus groups, 10+ years of ethnographic experience, and a review of validated depression scales used among diverse samples with good test-retest reliability (e.g., Beck's Depression Inventory, HAM-D, CES-D). The questionnaire contains most or all of the depressive symptoms contained in previous scales. The questionnaire was translated first into Spanish and then Tsimane by two bilingual Tsimane research assistants, ES and MG. To test the accuracy of the translation, the Tsimane questionnaire was back-translated into Spanish by a different Tsimane researcher, and discussions among the three bilingual Tsimane, ES and MG ensued until an effective translation was found that fully captured the essence of each item. All items were mutually intelligible to each Tsimane researcher when presented in Spanish versus Tsimane, despite fewer words in the Tsimane language. To minimize recall problems, participants were queried about prevalence of somatic and psychological symptoms associated with depression over the past month (including today), such as sadness, pessimism, changes in sleep and appetite, loss of interest in daily activities, diminished ability to concentrate, suicidal ideation and fatigue (see figure S1 for all items). Responses were given on an anchored scale where 1 corresponds to "rarely", 2 to "occasionally", 3 to "often", and 4 to "always." Although many respondents were previously unfamiliar with Likert-type scales, few were new to formal interviews because of their continuous participation in the Tsimane Health and Life History Project (THLHP) since 2002. Indeed, our long-term presence has helped to establish trusting, collaborative relationships among participants. Respondents were given a tutorial on the use of the scale, after which all individuals showed clear evidence of understanding the scale and the questionnaire. To gain ethnographic insight into factors affecting well-being beyond ordinal measures of mood, participants free-listed hypothetical lifestyle changes that would improve quality of life. Interviews were conducted in a private location in the Tsimane language by Tsimane researchers with multiple years of experience conducting anthropological and psychological interviews as part of the THLHP. Interviews were administered to 849 adults in 63 villages from 2007-2012. Response rate exceeded 90%. No Tsimane has ever taken medication to treat depression.

After the interview, the interviewer used the same 4-point scale to rate a subset of respondents based on his observations of the extent to which the respondent was laughing and smiling (jovial), and talkative during the interview and other THLHP interviews administered at the time (~45 minutes in total). This was done to help assess external validity of the questionnaire, as joviality and loquaciousness can reflect affective state, concentration and interest. Depression scores are significantly correlated with joviality in the expected negative direction (Spearman's rho=-0.35, p<0.001) and marginally correlated with loquaciousness (Spearman's rho=-0.11, p=0.072).

Demographics, anthropometrics, functional status and social conflict. Age, community membership and Spanish fluency were assessed during demographic interviews and annual THLHP census updates. Mean±SD age in the sample is 54±12 (range=32-90). Height and weight were measured during annual medical check-ups using a portable Seca stadiometer (Road Rod 214) and Tanita scale (BF680). As part of the THLHP's goal to assess changes in functional status in later adulthood, participants aged 50+ performed a modified battery of mild physical exercises originally used in the MacArthur Studies of Successful Aging (27). We coded whether subjects experienced any difficulty (yes=1, no=0) standing from a chair without using their arms, standing repeatedly, and balancing in the tandem position and on

each leg without using their arms or body. We also measured the time taken (in seconds) to walk three meters, pivot, and return as quickly as possible. Eleven measures were summed to create a “disability score” (mean±SD=11.3±2.9, range=5.5-21.0). To further assess functional status we asked all participants if they continued engaging in common, sex-specific subsistence tasks (continued participation=1, inability=0) and summed the measures to create a “subsistence involvement score”. For men this included four tasks: hunting, chopping big trees, walking all day and lifting heavy loads (male mean±SD=2.5±1.4, range=0-4), and for women three tasks: weaving bags, weaving mats and walking all day (female mean±SD=2.2±0.9, range=0-3). Finally, to assess social conflict, as part of the affect questionnaire participants were asked systematically whether they experienced any recent conflict across multiple dyads (e.g., conflict with non-kin, children) (yes=1, no=0) (see figure 4). We summed the measures to create a “social conflict score” (mean±SD=2.2±1.0, range=0-6).

Ethics statement. Procedures for all methods described here were approved by the UNM and UCSB Human Subjects Review Boards, Tsimane government, village leaders and study participants.

Data analysis. OLS regression is used to model proxies of functional status and low mood, and binary logistic regression is used to model likelihood of social conflict. Two items in the low mood questionnaire (irritability and indecision) were omitted from analyses since neither was significantly correlated with any other item and prevalence was low. Internal consistency of the 16-item low mood questionnaire slightly surpassed the standard benchmark of 0.7 (Cronbach’s alpha=0.71).

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