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Work to Live and Live to Work: Productivity, Transfers, and Psychological Well-Being in Adulthood and Old Age

Jonathan Stieglitz, Adrian V. Jaeggi, Aaron D. Blackwell, Benjamin C. Trumble, Michael Gurven, and Hillard Kaplan

INTRODUCTION

This paper considers psychological well-being in adulthood and old age, in light of the economic and social structure of the evolved human life history. Psychological well-being is the subject of significant scientific inquiry in large-scale modern societies (e.g., Easterlin, 2003; Blanchflower and Oswald, 2008; Diener and Chan, 2011), and it is often associated with economic productivity, social status, and network strength. However, very little is known about the evolutionary origins of mood variation or about mood variation during the course of human evolution. In fact, it has been suggested that depression is a maladaptive by-product of modern lifestyles due to inadequate pathogenic exposure in development, low physical activity level, high prevalence of metabolic disorder, or high levels of psychosocial stress from economic inequality, intense social competition, and residential isolation from kin (Raison et al., 2010; Rook et al., 2013).

One way to assess evolutionary implications of mood variation is to focus on small-scale societies. Small-scale societies possess similar socioecological features typical of the vast majority of human evolutionary history, including food insecurity, limited material wealth, and high pathogen burden coupled with little access to health care, but also frequent resource pooling, relative egalitarianism, and minimal social isolation. Research into psychological well-being in small-scale societies can (a) determine whether mood disorders exist, and if so, examine whether risk factors and buffers

are similar to those in modern societies, and (b) provide insight into the role of mood variation during humans' evolutionary history.

This paper has two goals. The first is to present an evolutionary framework for investigating the role of social relationships in affecting psychological well-being, and how it varies over the lifecourse and in different socioecological contexts. The second is to provide data on the prevalence and correlates of reduced psychological well-being and interpersonal conflict in a small-scale society, the Tsimane of Bolivia, to illustrate an empirical application of the framework. We hope to stimulate further research across populations and social contexts rather than offer a systematic review of the literature on psychological well-being.

Our central thesis is that flows of resources and assistance are critical in every phase of the human lifecourse and that psychological well-being responds to the nature and quantity of those flows. One universal feature of human life histories in small-scale societies is downward intergenerational resource flows (discussed in this volume by Lee, Hooper et al., and by Ellison and Ottinger; for original data, see Kaplan, 1994, and Kaplan et al., 2000, 2010; also see Lee, 2000, for data on the cross-cultural universality of downward flows within families). Children are net receivers of resources and assistance, whereas parents and grandparents are net givers during both reproductive and post-reproductive years. A second universal feature is the formation of marital bonds in which there is a flow of resources and assistance between spouses (see Hooper et al., this volume, and references cited therein). Resource flows from other kin and non-kin can also be important determinants of reproduction, health and mortality (e.g., Hawkes, 2003; Hill and Hurtado, 2009; Hill et al., 2009; Hrdy, 2009; Jaeggi and Gurven, 2013a).

We propose that deviations of those resource flows from expectations affect psychological well-being, both directly and indirectly. Resource flows can be disrupted for various reasons; one principal source of disruptions is the inability to provide support due to disability, illness, or some other permanent or temporary shock. Given that downward resource flows from older to younger individuals are expected in small-scale societies and that illness and disability become increasingly prevalent with age (see Gurven et al., 2012, for data on Tsimane forager-horticulturalists of Bolivia), we expect that the inability to provide expected resources will be a principal driver of reduced psychological well-being among adults, particularly as they age. Another principal source of resource flow disruptions is the intentional withholding of a resource, or resource diversions from expected recipients to other individuals or activities. In such cases, we expect interpersonal conflict to result, with downstream consequences for psychological well-being. Marriage may be particularly susceptible to such conflicts, given the possibility of pursuing reproductive and other interests outside of marriage.

This paper is divided into three parts. In the first part, we focus on psychological well-being in adulthood and old age, and on the direct effects of subsistence productivity on psychological well-being, as well as the indirect effects mediated by food and other resource transfers to kin. We illustrate the model empirically using demographic, epidemiological, and psychological data collected among a representative sample of adult Tsimane. In the second part, we consider conflicts due to resource diversions in marriage. We identify common sources of Tsimane marital conflict, most of which concern household productivity and transfers. In the third part, we compare our conceptual model to previous evolutionary and epidemiological models of depression and outline future research directions.

We conceptualize psychological well-being as a continuum from happiness to sadness, which are cross-culturally recognized emotions (Nesse, 1990). Understanding behavioral and physiological mechanisms underlying regulation of emotions across the continua of valence and arousal is an important goal for basic and clinical research (Holtzheimer and Mayberg, 2011). In this paper, we focus mostly on depression given its large contribution to the global burden of disease and over-representation in psychological well-being research (Whiteford et al., 2013). Although clinical depression in the United States has formal criteria defined by the Diagnostic and Statistical Manual of Mental Disorders, we use the term "depression" to refer to the cluster of symptoms often associated with depression (e.g., sadness, loss of interest). Depression is defined here as persistent sadness that interferes with routine daily functioning. We acknowledge that depressive symptomology may be highly variable across cultures, individuals, and within individuals over time, and that certain symptoms may have a higher sensitivity and specificity for identifying depression (due, for example, to symptoms such as fatigue frequently co-occurring with other morbidities) (Patel, 2001).

PART I. AN EXPLANATORY FRAMEWORK FOR PSYCHOLOGICAL WELL-BEING IN ADULTHOOD AND OLD AGE

Psychological Well-Being Varies with Determinants of Productivity

Our general hypothesis is that the ability to produce and transfer resources that have fitness value for self and kin is a primary determinant of psychological well-being in adulthood and old age (the "productive value" hypothesis). Food obtained from subsistence activities is necessary for growth, reproduction, and survival, and food production and transfer to descendants is a fundamental determinant of fitness in small-scale societies. Subsistence productivity is influenced by a vector of individual-level variables that affect strength and skill levels, including age, energetic status,

health status, and degree of physical limitations. In the absence of food storage or bank accounts, successful subsistence production relies heavily on cooperation and coordination with other group members to buffer risks of food shortfalls.

Forager diets consist largely of foods requiring high levels of strength and skill (Kaplan et al., 2000). Meat and other important foods (e.g., tubers, larvae, honey, nuts) require extraction from a substrate (often with technology), intensive processing, and assistance from others. Hunting return rates more than double from ages 20 to 40, even though strength peaks in the mid-20s (Walker et al., 2002; Gurven et al., 2006). Lags in peak efficiency relative to peak strength have also been documented for other foods, although not as extreme as hunting and not across all food types (Bird and Bird, 2002; Bock, 2002; Jones and Marlowe, 2002; Tucker and Young, 2005; Gurven and Kaplan, 2006; Crittenden et al., 2013; Stieglitz et al., 2013). The age-profile of net food production over the life-course appears to be fairly consistent across small-scale societies, with some variability in the onset of net productivity (Kaplan et al., 2000; Kramer, 2005; Hooper et al., this volume). Large caloric deficits are incurred early in life, and only by the mid- to late-teens do individuals start producing more calories than they consume. At this point, surplus caloric production increases with age, peaks in the 40s, and then slowly declines until dropping below consumption levels once again after seven decades. High adult productivity and kin-based residence enable net transfers from older to younger generations to bankroll prolonged juvenile dependency and to help promote transfers within generations during negative shocks (e.g., morbidity that inhibits work). These transfers increase the likelihood that juveniles reach adulthood, allow parents to rear multiple dependent offspring simultaneously, and reduce adult mortality (Lancaster and Lancaster, 1983; Jaeggi and Gurven, 2013a).

Despite frequent resource pooling to buffer risk, exposure to periods of uncertainty in the food supply was probably common over human evolutionary history. Food anxiety[1] is a commonly reported major life stressor cross-culturally and is associated with several indicators of reduced psychological well-being (e.g., anxiety, depression) (Pike and Patil, 2006; Hadley and Patil, 2008; Weaver and Hadley, 2009). Because the ability to produce and transfer food is strongly age-dependent, prevalence of food anxiety should vary with age, independently of other factors including household need and availability of social support. Food anxiety should also vary with energetic status, since nutrient deficiencies may directly affect psychologi-

[1]We use the term "food anxiety" to signify psychological distress over lack of food security. The 1996 World Food Summit defined food security as existing when people, at all times, have access to sufficient, safe, and nutritious food to maintain a healthy and active life.

cal well-being. For example, micronutrient supplementation reduces levels of perceived stress and anxiety in nonclinical Western samples (Long and Benton, 2013). Nutrient deficiencies may also indirectly affect psychological well-being by reducing the capacity to work and subsistence productivity (see below).

Demonstrating a link between productivity and psychological well-being, Figure 9-1 shows the probability of reporting food anxiety by age among Tsimane adults aged 20+, alongside the age-profile of Tsimane net daily caloric production. Food anxiety is prevalent overall (31 percent of adults), and more prevalent among younger adults, despite low household dependency and few deleterious effects of senescence on the ability to produce food. Food anxiety sharply declines with age, as productivity increases, and reaches a nadir at age 46, the same age that productivity peaks. There

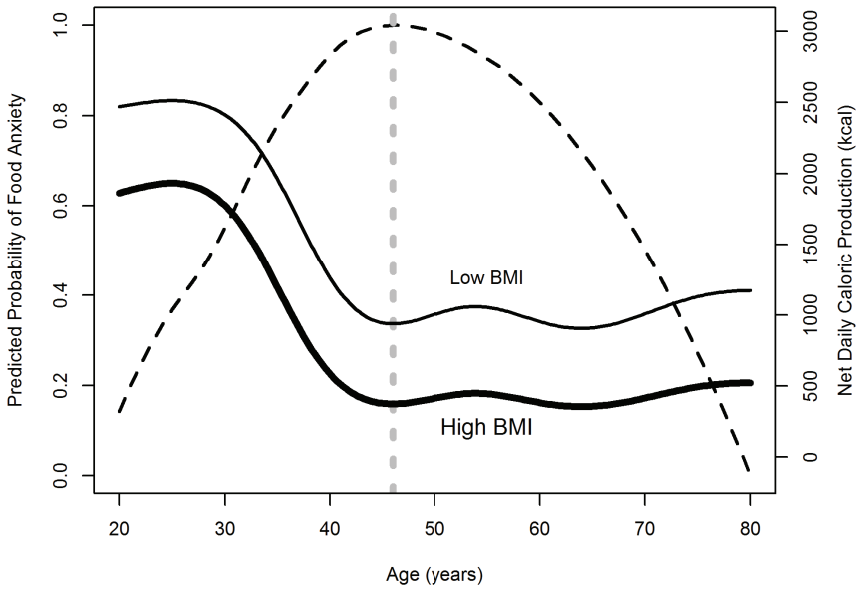

FIGURE 9-1 Predicted probability of reporting food anxiety by age and BMI among Tsimane.

NOTES: Generalized additive mixed model, controlling for sex and repeated measures, n = 1002 adults, 1137 observations. BMI is plotted at 2 SD below and above the mean (mean ± SD = 24 ± 3). Age thin plate spline $p<0.001$, edf = 5.814, $B_{Male}= -0.31$, $p = 0.02$, $B_{Bmi} = -0.077$, $p<0.001$. Tsimane daily net food production (production minus consumption) is shown on the second y-axis (averaged across sexes). The nadir in food anxiety corresponds to the age of peak productivity (dashed vertical line).

is also a main effect of body mass index (BMI) in the predicted negative direction: Tsimane with higher BMI report lower levels of food anxiety than Tsimane with lower BMI (BMI range = 16-38). At the age of peak productivity, probability of food anxiety is over twice as high for Tsimane with low versus high BMI (0.34 vs. 0.16).[2] Although food anxiety appears to increase slightly at older ages, this increase is not significant (OR/year = 1.03, $p = 0.13$, including ages ≥ 60 and controlling for sex and BMI). Food anxiety may not increase at older ages as productivity declines because of declining caloric dependency of offspring and grandoffspring (Gurven and Kaplan, 2007).

Aside from food anxiety, other indicators of psychological well-being[3] vary predictably with the ability to produce and transfer resources, as determined by age and energetic status. We find that the Tsimane depression score increases with age among adults aged 18+ (controlling for sex, not shown), peaking in the late 70s when caloric production approaches pre-adult levels. Depression score, like food anxiety, is inversely associated with BMI and rises more steeply with age among those with lower BMI (not shown). Large body size may partly offset deleterious effects of aging on psychological well-being by supporting greater subsistence productivity and resource transfers. For example, only 59 percent of Tsimane women aged 65+ report being able to get materials from the forest and weave a mat if below median BMI, compared to 83 percent of age-matched women at/above median BMI ($\chi^2 = 5.08$, $p = 0.024$, $n = 73$). Among men aged 65+, only 6 percent report being able to lift a quintal of rice (~46 kilograms) if below median BMI compared to 22 percent of age-matched men at/above median BMI (Fisher's Exact Test $p = 0.046$, $n = 89$).

Morbidity is another important impediment to subsistence productivity and food transfers, in addition to age-related physical decline and reduced energetic status as described above. Empirical links between morbidity

[2]While BMI may be inversely associated with food anxiety in small-scale societies, BMI may be positively associated with food anxiety in large-scale modern societies. In modern societies food anxiety is similarly associated with reduced productivity (e.g., low socioeconomic status or SES), but because low SES is also associated with obesity, positive associations between BMI and food anxiety emerge.

[3]To evaluate depression, we developed a culturally appropriate 16-item interview 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 (Beck's Depression Inventory, HAM-D, CES-D). The interview contains most or all of the symptoms contained in previous scales. Adults aged 18+ (mean ± SD age = 54 ± 12) were recruited regardless of their health status, and no individual refused participation. Participants were queried about prevalence of symptoms over the past month (e.g., sadness, guilt, fatigue, changes in sleep or appetite). Responses were given on a self-anchored scale from 1 ("rarely") to 4 ("always"), and items were summed to create a "depression score" (mean ± SD = 38.3 ± 6.8, range = 19-60, n = 849 men and women) (refer to Stieglitz et al., 2014, for further methodological details).

and reduced psychological well-being are well documented cross-culturally (Cohen et al., 2007; Diener and Chan, 2011; Fagundes et al., 2012; Yanek et al., 2013). We hypothesize that morbidity is causally implicated in the onset and maintenance of reduced psychological well-being. Indeed, Tsimane depression score varies predictably with self-reported health: adults aged 18+ reporting "extremely poor" overall health score 14 percent higher in depression, on average, than adults reporting "very good" health after controlling for potential confounds such as age, sex, BMI, Spanish fluency, and residential proximity to town (marginal mean depression score = 40.4 vs. 35.3, $p = 0.026$, $n = 579$). Less than 1 percent of Tsimane adults aged 18+ report "excellent" overall health, highlighting the pervasiveness of morbidity and its potential to impair psychological well-being in societies with limited access to healthcare. Clinical data indicate that <10 percent of Tsimane adults aged 18+ are diagnosed as "healthy" in a given year.[4] Common diagnoses include gastrointestinal, respiratory, and skin infections, and arthritis. Older adults also commonly report disrupted sleep quality due to persistent musing over poor health (self or kin) (Gandhi Yetish, personal communication). Poor sleep quality may delay recovery and facilitate a cycle of morbidity, disability, and reduced psychological well-being.

Across diverse societies, subjective well-being varies positively with self-reported health (see Table 9-1). We propose that this relationship may be especially tight in energy-limited subsistence societies, where direct effects of physical condition on production may be stronger relative to sedentary industrialized societies. Managing disability-related production shortfalls with modern technology (e.g., glasses, hearing aids) or by liquidating savings accounts are not options in small-scale societies. In modern societies, unemployment (analogous to reduced subsistence productivity in small-scale societies) is a major cause of depression (Paul and Moser, 2009). Yet even in modern societies with government-subsidized unemployment benefits, employer- subsidized sick leave, or health insurance, functional limitations due to illness, injury, or senescence commonly reduce quality of life.[5] Links between functional limitations and reduced psychological well-being appear to exist in other species, too. For example, captive animals deprived of opportunities to perform preferred behaviors present signs of withdrawal that are similar to signs observed in addictive drug deprivation (Boissy et al., 2007).

[4]Bolivian physicians diagnosed patient illnesses during annual medical exams as part of the Tsimane Health and Life History Project (THLHP). Diagnoses from the International Classification of Disease (ICD-10) were grouped into gastrointestinal, respiratory, and other ailments for exams conducted from 2002 to 2004. "Healthy" is defined here as not presenting any symptom associated with any ICD-10 code.

[5]Reduced functional ability is increasingly contributing to the global burden of disease, as life expectancies increase, populations age, and the number of disabled individuals increases (National Institute on Aging, 2007).

TABLE 9-1 Mean Subjective Well-Being Score (shown as % maximum possible score) by Self-Reported Health from the Multisite Project AGE

Economy	Site (n)	Self-Reported Health			% increase in subjective well-being from poor/fair to excellent health
		Poor/fair	Average/good	Excellent	
Pastoralist	Botswana (174)	37	53	62	68
Market-rural	Momence, IL, USA (207)	70	77	80	14
Market-rural	Clifden, Ireland (129)	73	80	83	14
Market-suburban	Swarthmore, PA, USA (200)	73	78	82	12
Market-suburban	Blessington, Ireland (170)	72	75	82	14
Market-urban	Hong Kong (192)	57	57	67	18

NOTE: Well-being scores were collected among adults aged 18+ using a modified Cantril Self-Anchoring Ladder. Respondents were asked to select their current position on the ladder, with the highest and lowest steps representing the best and worst possible lives, respectively.
SOURCE: Adapted from Table 5.4 of Keith et al. (1994).

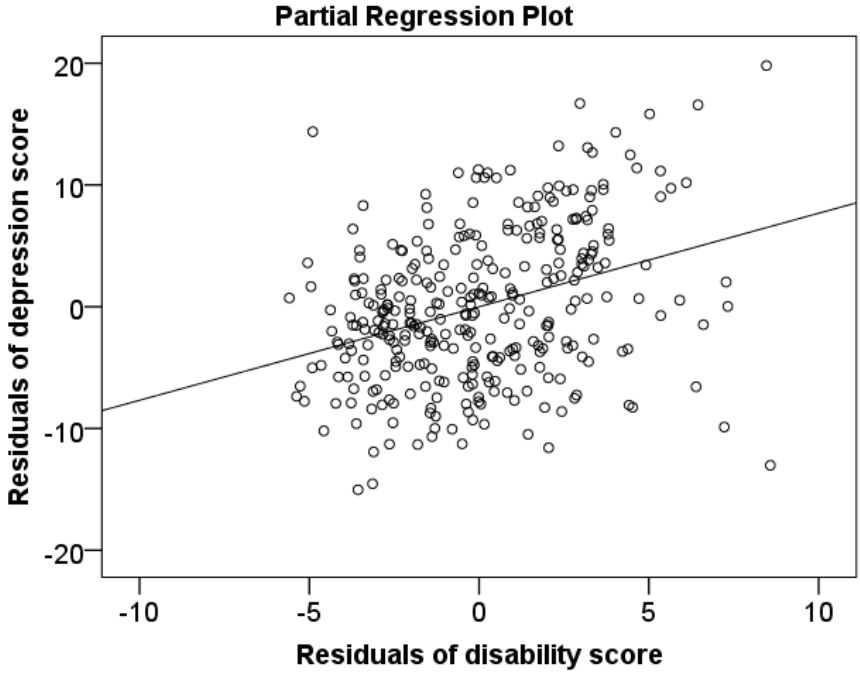

FIGURE 9-2 Depression is associated with greater physical limitations among Tsimane aged 50+.
NOTE: N = 325, controlling for age, sex, BMI, Spanish fluency, and village distance to the market town of San Borja. Methodological details are provided in footnotes.

Like morbidity, functional limitations can reduce inclusive fitness through multiple pathways including reduced subsistence production, kin transfers, and reproductive opportunities. Functional disability is a strong predictor of Tsimane depression: Adults aged 50+ in the top decile of disability[6] score 14 percent higher on depression than those in the bottom decile after controlling for potential confounders ($p<0.001$) (see Figure 9-2).

[6]As part of the THLHP's monitoring of functional status in later adulthood, participants aged 50+ performed a modified battery of mild exercises originally used in the MacArthur Studies of Successful Aging. 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 the arms or body. We also measured 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 = 11.2 ± 2.9, range = 5.5-21.0, n = 325 men and women).

Tsimane perceptions of how to improve quality of life support a strong, potentially bi-directional link between productivity and psychological well-being. When we asked 723 adults aged 40+, "If you could change something in your life to make you happier, what would you change?" *higher subsistence productivity* and *lower frequency of illness* were the most common responses for both sexes. Iraqw and Datoga women of rural Tanzania similarly report hunger and morbidity as major life stressors (Pike and Patil, 2006). Indeed, across diverse societies, cross-sectional and longitudinal studies have documented strong positive associations between functional status and psychological well-being (Ormel et al., 1994; Covinsky et al., 2010; Lindwall et al., 2011). We hypothesize that this relationship is mediated in part by resource transfers, as greater functional ability increases economic productivity and the extent of food and other transfers to both kin and non-kin.

Resource Transfers Mediate the Effect of Productivity on Psychological Well-Being

Preferential sharing partnerships are common in small-scale societies, and individuals generally share less with those who give less (Jaeggi and Gurven, 2013a; Jaeggi and Gurven 2013b).[7] Indicators of productivity and generosity are thus highly valued by both sexes in both same- and opposite-sex partnerships. Hunting performance and meat sharing may be two of the most important routes to prestige and status among men in hunter-gatherer societies (Kaplan and Hill, 1985; Hawkes and Bliege Bird, 2002; Smith, 2004; Gurven and Von Rueden, 2006; Von Rueden et al., 2008). Similarly, women's desirability as a social partner (as perceived by other women) increases with reputation of being hard-working and a good mother (Rucas et al., 2006). Across cultures, preferred mate characteristics including dependability, emotional stability, maturity, good health, and intelligence (Buss et al., 1990) are reliable and valid indicators of current and future productivity for both sexes.

Given fitness benefits of high social status and mate value (see Von Rueden et al., 2008, 2011, and references therein), gaining recognition as a high producer and as generous might be a psychological goal in many cultures. Providing support to others can increase support received, especially during periods of greater need (Gurven et al., 2000), thus increasing resilience to negative shocks including illness or injury. Consistent with the gaining-recognition hypothesis, providing support appears to increase

[7]Contingency is important in sharing relationships, but dyadic imbalances may be common in the short or long term since sharers may subsequently receive from multiple parties (recipients or nonrecipients) and since exchange may consist of multiple currencies.

well-being regardless of whether aid is reciprocated. For example, among older married Americans, self-reported support provided to others (kin and non-kin) in the form of assistance with daily tasks and emotional support reduced risk of mortality prospectively, even after controlling for support received (which did not consistently affect mortality risk) and other confounders (Brown et al., 2003). Similarly, older American adults with greater self-perceptions of "generativity" (concern for the well-being of others) engage more frequently in socializing and providing support, and are also less likely to experience functional disability prospectively (Gruenewald et al., 2012). In contrast, net dependence among older adults may increase risk of depression and may further impair functional status rather than improve it (Seeman et al., 1996; Liang et al., 2001). "Feeling burdensome" to others providing support is associated with depression among younger and older American adults (Brown et al., 1999; Liang et al., 2001). Together these results suggest a positive association between support given and received, and between net support given and psychological well-being.

Prolonged social isolation in adulthood was probably rare over human evolutionary history given high fertility, frequent resource pooling, and minimal privacy in kin-based residential groups. While there is some ethnographic evidence of "elder neglect" and practices facilitating hastening of death among frail "net consumers," there is also evidence that such decisions are made by elders themselves, suggesting few conflicts of interest (Glascock, 2009). In predemographic transition societies, net food flows are downward, from grandparents to parents to children, and grandparents may also provide nonmaterial contributions by resolving conflicts or adopting roles as leaders, orators, and shamans (Keith et al., 1994; Hawkes, 2003; Gurven and Kaplan, 2006; Kaplan et al., 2010; Gurven et al., 2012). Given a modal age of adult death of about 70 among foragers and forager-horticulturalists (Gurven and Kaplan, 2007), few adults live long enough to be a net burden on kin. This could minimize risk of interpersonal conflicts over time and resource allocations, and risk of social isolation. Whether reduced ability or willingness to provide material or nonmaterial support increases risk of loneliness remains unexplored in small-scale societies. However, in a random sample of private residences in the Netherlands, Gierveld and Dykstra (2008) found an inverse association between number of generations supported (financially, emotionally, or instrumentally) and degree of loneliness after controlling for potential confounders. Perceived or real lack of social support and loneliness are well-documented predictors of reduced well-being in modern societies (Steptoe et al., 2013; Teo et al., 2013). The effect of social isolation on mortality risk may even rival effects of well-established risk factors such as smoking, hypertension, and obesity (House et al., 1988; Holt-Lunstad et al., 2010).

In sum, available evidence from small-scale societies suggests that risk of depression increases with age, as health, functional ability, and productivity decline, and is not characterized by a "mid-life crisis" as in modern societies (Blanchflower and Oswald, 2008). There is increasing recognition worldwide that depression among the "oldest old" (age 85+) may be more common than previously thought (Luppa et al., 2012), yet depression is not an inevitable aspect of aging. Functional ability is an important mediator of age-related change in psychological well-being cross-culturally (Kunzmann et al., 2000; Fiske et al., 2009; Stieglitz et al., 2014). Aside from lowering productivity, functional disability may reduce investment in reciprocal sharing relationships, social status, and mate value, which can independently reduce psychological well-being.

In the next part, we consider marriage as a reciprocal relationship uniquely poised to influence psychological well-being given the central role of production and kin transfers. We focus on the extent to which marital conflict over appropriate levels of paternal investment may affect mental and physical well-being of reproductive-aged women.

PART II. SEXUAL COOPERATION, CONFLICT, AND PSYCHOLOGICAL WELL-BEING

Marriage[8] is a human universal and probably the most complex cooperative relationship that humans form. Marriage involves coordinated resource production and distribution, child care, sexual responsibilities, and novel opportunities for resource transfers within and among families. Marriage is a fundamental form of risk buffering as it facilitates a sexual division of labor necessary to provide the adequate complement of resources upon which humans rely. In modern societies, entering into marriage may improve psychological well-being relative to remaining single, particularly early in the union (Musick and Bumpass, 2012). Marital problems can reduce household productivity, increase risk of union dissolution, and potentially affect fitness outcomes for both parental and non-parental caregivers. Self-reported marital problems predict depression for both sexes (Kiecolt-Glaser et al., 1987; Choi and Marks, 2008). Common causes of divorce worldwide include conflicts over relative work effort of either partner, how fruits of labor are divided, and pursuit of extramarital affairs (Betzig, 1989).

Life history models acknowledge cooperative and conflictive elements of marriage (e.g., Borgerhoff Mulder and Rauch, 2009; Gurven et al., 2009; Holland Jones and Ferguson, 2009). These models borrow from household

[8] "Marriage" refers here to any sexual pair-bond, including noncohabiting and cohabiting relationships.

bargaining models in economics (Himmelweit et al., 2013) and illustrate how partners may negotiate investment decisions both within and outside of marriage. Although empirical studies of the causes and consequences of marital conflict in small-scale societies are rare, Stieglitz et al. (2011, 2012a) have recently shown that men's diversion of household resources (e.g., through infidelity) is the most prominent source of intense conflict within Tsimane couples (see below). Throughout the developing and developed world, men are more likely than women to commit infidelity and squander household resources (Haddad et al., 1997; Atkins et al., 2001). Next we briefly review the logic underlying life history models of bargaining in marriage, and we highlight how sex differences in embodied, relational, and/or material capital may affect household decision-making and maternal well-being.

Marital Cooperation and Conflict in Small-Scale Societies

Several features of human life histories increase costs to both sexes of switching marital partners, including prolonged offspring dependency, rearing multiple dependents simultaneously, and intense bi-parental provisioning and care of offspring (Winking et al., 2007; Lancaster and Kaplan, 2009). Marriage enables men and women to attain fitness benefits through joint production of offspring, which produces an economy of scale such that the fitness of the pair exceeds the summed fitness of solitary partners. Children are a shared public good in the sense that they are a fitness outcome for both partners, regardless of the investment each provides. Our principal hypothesis is that a primary determinant of marital conflict and reduced psychological well-being of at least one partner in the union is the diversion or withholding of resources by one partner that the other partner expects. We also hypothesize that differential bargaining power between the sexes determines both the extent and resolution of marital conflict.

In small-scale societies lacking material wealth, bargaining power derives from an array of embodied and relational characteristics (e.g., body size, skills, coalitional support). Given men's greater size and strength, intimate partner violence (IPV) may be used as a "bargaining chip" to strategically leverage a selfish outcome, despite potential costs to the victim, aggressor, and offspring. Recently Stieglitz et al. (2011, 2012a) have argued that men use physical violence in marriage to control women's responses to the diversion of household resources, often in pursuit of extramarital affairs (hereafter paternal disinvestment). IPV functions to quell women's objections to paternal disinvestment, maintain maternal investment, and dissuade women from pursuing relationships with other men. Among Tsimane, 85 percent of married women report ever experiencing IPV (n = 110), despite a lack of formal patriarchal institutions and poten-

tial risks to abusive husbands of physical retaliation or economic sanctions (e.g., reduced food or labor sharing). Roughly 60 percent of violent incidents directed toward wives (n = 124) occur during arguments over paternal disinvestment. Physical coercion can enhance male bargaining power by undermining women's productivity or social ties, thus limiting women's options in or outside of marriage. Well-established health consequences for women experiencing abuse (physical or emotional) include depression and other mental disorders.

Relational capital can increase women's marital bargaining power. Close proximity of the wife's natal kin per se does not increase the extent to which spousal interests converge, but can influence whose interests prevail in negotiations (e.g., Sear and Mace, 2008). One might expect matrilocal residence to improve women's psychological well-being through multiple pathways in semi-nomadic, bi-local societies. Matrilocal residence is associated with increased paternal investment, decreased self-reported marital strife for men and women, and reduced risk of IPV against women (Erchak, 1984; Counts et al., 1999; Stieglitz et al., 2011). Beneficial effects of matrilocal residence on maternal psychological well-being may be especially salient during times of increased household demand (e.g., following birth). Future research should determine behavioral and physiological mechanisms underlying the association between residential status and maternal and child well-being, and the relative importance of various alloparental inputs (e.g., food, childcare, advice) in affecting well-being, especially among new mothers.

Market Integration Can Exacerbate Gendered Inequalities in Resource Access

In high fertility societies with minimal access to contraception, market integration provides novel opportunities for conflict over men's parental investment decisions, with direct implications for household well-being. Market integration may take several forms including town visits, schooling, sale of subsistence goods, and itinerant wage labor. Wage opportunities are often sporadic and incompatible with provisioning of high-quality childcare because they entail risk or require extended travel and village absenteeism. This discourages women's market participation and increases women's dependence on men for critical market goods and services. Gendered inequalities in access to market wealth can increase the degree of coercive control used and tolerated in marriage. Solitary labor migration mitigates reputational risk of paternal disinvestment (if unknown to others), inhibits retaliation by wives and other interested parties, and may create desires among men for extramarital partnerships to relieve loneliness (Smith, 2007; Wardlow, 2007). Money is fungible, liquid, seldom saved, disproportion-

ately controlled by men, and can easily be squandered at substantial cost to the family without directly risking marital dissolution. Economists have long recognized that reallocating income from fathers to mothers increases children's consumption, nutritional status, and well-being; increases in men's income result in greater expenditures on tobacco and alcohol more than increases in women's income (Haddad et al., 1997).

Tsimane wives often accuse husbands of improper use of wages, resulting in arguments that increase women's risk of experiencing IPV (Stieglitz et al., 2011, 2012a). Unpublished results confirm high levels of wage diversions by married men, although there is much inter-individual variability. In a 2010 survey conducted among men in a village near the market center, 59 percent (20/34) report ever pursuing commercial sex opportunities (9 percent report 1 instance, 29 percent 2-5, 3 percent 6-9, and 18 percent ≥10 instances). Wage diversions bear direct health consequences for wives. For example, we find that relative to wives in remote villages, wives residing near the market center experience greater likelihood of trichomoniasis, a sexually transmitted infection (STI), despite having easier access to modern healthcare and schooling (Stieglitz et al., 2012b). Tsimane women's risk of STI appears to be independent of their own sexual behavior, which is consistent with prior research in the developing world identifying men's extramarital sexual behavior as a major source of HIV infection among wives (Silverman et al., 2008).

In sum, in the case of the Tsimane, men's withholding of parental investment and diversion of time and resources away from the family (especially in pursuit of extramarital sex) are the most common causes of marital conflict and of physical wife abuse. Sexual conflict over parenting effort appears to increase with market integration and fungible resources for mating effort. At present, we cannot determine empirically whether marital conflict is a source of reduced psychological well-being in adults (and perhaps children, through the indirect effects mentioned above). We suspect that this is the case in light of the fact that worldwide, maternal anxiety, depression, and post-traumatic stress disorder appear to be prevalent mental-health sequelae of reduced family functioning (Campbell, 2002). Yet despite potential costs to women and children of paternal disinvestment, maternal resilience is highly variable and responsive to socioecological factors influencing the importance of bi-parental care and the availability of kin. The extent to which conflict over paternal disinvestment affects maternal well-being, therefore, depends in part on women's alternative sources of parental investment.

PART III. EXISTING MODELS OF DEPRESSION AND FUTURE RESEARCH DIRECTIONS

Darwin hypothesized that mood and emotion[9] evolved by natural selection to motivate responses to recurring adaptive problems (Darwin, 1872). Positive valence motivates continuation of prior behaviors associated with its occurrence, while negative valence motivates disengagement and pursuit of alternative strategies (Seligman, 1975; Nesse, 2000). The productive value hypothesis developed here posits that depression is a consequence of reduced ability to produce and transfer resources that are valuable to self and/or kin (see also Stieglitz et al., 2014). The second corollary hypothesis is that the withholding or diversion of resources, relative to expectations of transfers, causes conflict with downstream negative impacts on psychological well-being. Table 9-2 provides a summary of other approaches to depression within an evolutionary framework. While there are some important differences among these approaches, the productive value hypothesis helps unify and organize several shared features.

The common finding across cultures that support given to others and "feeling needed" are associated with indicators of greater mental and physical well-being (e.g., Brown et al., 2003; Gierveld and Dykstra, 2008; Gruenewald et al., 2012), which is consistent with a human life history perspective emphasizing the importance of downward net resource transfers in adulthood and old age. Suicide, an extreme manifestation of depression, may be more likely to occur among individuals who are a net burden on kin (de Catanzaro, 1984, 1991). Depression and suicide may therefore mitigate inclusive fitness losses among individuals who extract more resources than they provide (Brown et al., 1999). This "avoiding obsolescence" hypothesis of depression is consistent with the logic of our more general hypothesis linking resource production, distribution, social relationships with kin and non-kin, and psychological well-being. Whether depression helps individuals devise novel strategies for increasing one's industriousness or utility in other domains during periods of declining caloric productivity, thereby reducing the net burden on kin, merits further consideration.

Several adaptive models posit that depression functions primarily to elicit social support, which suggests increased psychological well-being following support received (Table 9-2). For example, depression is hypothesized to solicit greater investment from a social partner by imposing costs on that partner (the "labor strike" hypothesis) (Hagen, 1999, 2002, 2003); avoid exclusion from vital social relationships (Allen and Badcock,

[9]Compared to emotions, moods are longer in duration and more indirectly associated to specific cues.

TABLE 9-2 Summary of Previous Evolutionary Hypotheses of Depression

Hypothesis (source)	Benefit of Depression	Some Evidence for Hypothesis
1. Avoiding obsolescence (Brown et al., 1999; de Catanzaro, 1984, 1991)	Minimizes inclusive fitness losses via withdrawal.	Depression, hopelessness, suicidal ideation, and suicide attempts are associated with perceptions of being a burden on kin.
2. Bargaining/"labor strike" (Hagen, 1999, 2002, 2003)	Imposes costs on others as a negotiating tactic designed to improve one's circumstances.	Post-partum depression in women is associated with increased paternal investment.
3. Reduced social risk (Allen and Badcock, 2003)	Avoids exclusion from vital social relationships by inhibiting risk-taking and competitive desire.	Depression is associated with inadequate social support (perceived or real).
4. Analytical rumination (Andrews and Thomson, 2009; Watson and Andrews, 2002)	Ensures availability of cognitive resources to focus attention on problem solving.	Depression is associated with persistent musing over problems prompting the depressive episode.
5. Effective goal pursuit (Nesse, 2000; Price, 1994)	Prompts disengagement from unproductive efforts, including social competition.	Depression is common among those pursuing "unreachable goals," or following defeat in competition.
6. Pathogen host defense (Anders et al., 2013; Raison and Miller, 2012)	Conserves metabolic resources to promote immune defenses against pathogens.	Depression is associated with greater immune activation.

2003); and improve one's ability to solve social or other problems through rumination (Watson and Andrews, 2002; Andrews and Thomson, 2009). Yet the hypothesis that receiving support improves either mental or physical well-being has not been supported empirically (Seeman et al., 1996; Liang et al., 2001; Brown et al., 2003). In light of the Tsimane findings, the links between supports given and received (perceived and real) in core cooperative relationships, the degree and resolution of interpersonal conflicts, and psychological well-being merit further consideration. In addition, whether depression "serves" to elicit support, or is simply an outcome of not receiving it, remains unclear.

As mentioned in the Introduction, a different perspective interprets depression as a maladaptive byproduct of modern lifestyles. This "im-

mune dysregulation hypothesis" posits that reduced infectious microbial exposure during development in Western settings contributes to insufficient anti-inflammatory signaling, which promotes hyper-inflammatory responses to psychosocial or other stressors and induces depression (Raison et al., 2010; Rook et al., 2013). It may be that these factors exacerbate the risk of depression, but we find that reduced subsistence productivity and resource transfers are associated with depression in a small-scale society.

Prospective studies of the causes and consequences of depression are necessary to test unique predictions derived from alternative hypotheses. Empirical evidence that depression leads to improved outcomes (e.g., repaired social relationships) is actually quite scarce. In fact, contrary to this logic, history of psychological disorder is a strong predictor of subsequent psychological disorder (Kuh et al., 1997). It therefore remains unclear whether depression serves an adaptive function, or whether depression is a pathological extreme of an adaptive mood continuum. Given that depression may not be necessary to combat infection or negotiate social relationships, and that depression may not be reversible even if health or social conditions improve, an adequate adaptive theory must explain why natural selection would favor a depressed phenotype given the costs in a highly social species. A major opportunity cost of depression is foregone economic productivity, yet few hypotheses acknowledge that opportunity costs of depression (and whether depression manifests) may be variable within an individual over time, as productivity and the ability to impact well-being of kin change.

Directions for Future Research

This paper provides a framework for linking social relationships and social context to psychological well-being in adulthood. The central prediction is that deviations from expected flows of resources and assistance affect well-being. We emphasize disruptions in resource flows via two routes: (1) the inability to produce and transfer resources, and (2) resource withholding or diversion. The factors affecting each of those two sources are likely to vary over the lifecourse and by context.

One direction for future research is on how social context affects psychological-well-being through the first route. How do expectations about transfers vary by age, gender, SES, social network, region, and other factors? What are the primary determinants of those expectations? What factors affect within-population variance in the ability to provide expected transfers, and the willingness to provide transfers at similar levels of ability? Does the lack of recipients of transfers (for example, due to childlessness or distance) have the same effects on well-being as the inability to produce and transfer resources? Do impediments to the ability to produce and transfer

resources have purely additive impacts on psychological well-being, or do they interact with other social factors, such as community involvement and government subsidies?

With respect to the second route, similar questions can be asked about expectations, the determinants of their variability, and within-population variation. We have focused primarily on interpersonal conflicts in marriage, derived largely from deviations in expected paternal investment, but the links between expectations, conflict, and psychological well-being merit further investigation. There appears to be significant variability in the degree of psychological resilience in the context of family adversity (e.g., Patterson, 2002). What factors affect bargaining power within the family, and how do those factors shape both the likelihood of conflict and the downstream psychological consequences of those conflicts?

Last, in this paper we have focused primarily on the family and broader kin relationships, because of their centrality in the lives of people. However, as mentioned above, social embeddedness goes beyond the family and kin group. Investigating the relationship between expectations of transfers and psychological well-being in other relationships is likely to be fruitful. Future research should consider the broad scope of social exchange networks across a variety of currencies (e.g., calories, money, information) (Kaplan and Gurven, 2005; Jaeggi and Gurven, 2013b).

CONCLUSION

The productive value hypothesis attempts to explain behavioral mechanisms underlying mood regulation across the continua of valence and arousal, while recognizing that stressors and stress responses vary by phenotypic condition, across life stages, and across ecologies. While this framework requires more development (e.g., we do not consider the role of heritability or identify physiological mechanisms), it is the first to explicitly link physical health, productive capacity, sociality, and mental health in small-scale societies.

Depressive symptomology appears to be regularly experienced under conditions more similar to the ones in which humans evolved and is not simply a by-product of modernity. Poor health appears to be causally implicated in the onset of depression cross-culturally,[10] yet not all sick individuals experience depression. Understanding factors that promote resilience to chronic morbidity and adverse life events is an important scientific and practical goal, as much of the world's population lives in poverty.

[10]The association may be bi-directional (e.g., if depression induces alcoholism or other adverse health behaviors).

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