



Contents lists available at ScienceDirect

Physiology & Behavior

journal homepage: www.elsevier.com/locate/physbeh

Parental hormones are associated with crop loss and family sickness following catastrophic flooding in lowland Bolivia

Benjamin C. Trumble^{a,b,*}, Jonathan Stieglitz^c, Adrian V. Jaeggi^d, Bret Beheim^e,
Matthew Schwartz^f, Edmond Seabright^f, Daniel Cummings^f, Hillard Kaplan^g, Michael Gurven^h

^a School of Human Evolution and Social Change, Arizona State University, USA

^b Center for Evolution and Medicine, Arizona State University, USA

^c Université Toulouse 1 Capitole, France

^d Department of Anthropology, Emory University, USA

^e Department of Anthropology, Max Planck Institute, Leipzig, Germany

^f Department of Anthropology, University of New Mexico, USA

^g Health Economics and Anthropology & Economic Science Institute, Chapman University, USA

^h Integrative Anthropological Sciences, University of California-Santa Barbara, USA

ARTICLE INFO

Keywords:

Testosterone

Cortisol

Natural disaster

ABSTRACT

The physiology of fatherhood is a growing field of study, and variability in hormonal mediators of reproductive effort (e.g. testosterone, cortisol) can predict variability in paternal investment. Studies often find that lower testosterone levels are associated with increased paternal investment, though most studies are conducted under relatively stable ecological conditions. In this paper, we examine parental physiological correlates of crop loss and family health problems among Tsimane forager-horticulturalists following a catastrophic flood in lowland Bolivia. Immediately after a devastating 2014 flood that impacted > 75% of Tsimane communities, we conducted structured interviews examining crop losses and morbidity, and collected saliva specimens from 421 parents (n = 292 households) to analyze cortisol and testosterone. Over 98% of interviewees reported horticultural losses, with the average family losing 88% of their crops, while 80% of families reported flood-induced injuries or illnesses. Controlling for age, body mass index, and time of specimen collection, men's testosterone was negatively associated with both absolute cropland losses (Std. $\beta = -0.16$, $p = 0.037$), and percent of cropland lost (Std. $\beta = -0.16$, $p = 0.040$). Female testosterone was not associated with crop losses. Using the same control variables, both male and female cortisol was negatively associated with a composite measure of child health burden (fathers: Std. $\beta = -0.34$, $p < 0.001$; mothers: Std. $\beta = -0.23$, $p = 0.037$). These results are discussed in the cultural context of a strong sexual division of labor among Tsimane; we highlight the physiological and psychosocial costs of experiencing a natural disaster, especially for paternal caregivers in a nutritionally and pathogenically stressed subsistence population where cultigens provide the majority of calories in the diet.

1. Introduction

Natural disasters (e.g. flooding, drought) are often part of broader ecological shifts that precede evolutionary change, including the origin of the genus *Homo* [1,2]. The human commitment to extensive resource transfers between and within generations [3–5] likely mitigated deleterious fitness effects of historically common environmental shocks. While most anthropological research in small-scale foraging and mixed foraging-horticultural societies has focused on ways in which individuals cope with variability in daily resource acquisition [3,5,6], much less is known about how individuals cope with natural disasters

that impact large geographic areas and segments of the population. The irregular occurrence of natural disasters, logistical difficulties of accurately assessing losses from and responses to disasters in remote areas, and the fact that behavioral and physiological responses are not preserved in the fossil record all make it difficult to infer how individuals in small-scale societies cope with natural disasters. To date, little is known about physiological and behavioral effects of natural disasters, or the extent of resilience in small-scale societies operating largely “off-the-grid”.

In this paper we: i) document crop losses and family health problems (i.e. illness and injury) following a recent catastrophic flood in

* Corresponding author at: School of Human Evolution and Social Change, Arizona State University, USA.
E-mail address: trumble@asu.edu (B.C. Trumble).

<https://doi.org/10.1016/j.physbeh.2018.02.028>

Received 19 August 2017; Received in revised form 12 February 2018; Accepted 14 February 2018
0031-9384/ © 2018 Elsevier Inc. All rights reserved.

lowland Bolivia among Tsimane forager-horticulturalists and ii) examine physiological correlates (i.e. testosterone and cortisol) of crop loss and family health problems among Tsimane parents. Hormones such as testosterone and cortisol are often used to track levels of physiological or psychological arousal [7]. Testosterone is associated with paternal investment in humans and other primates [8–12], and its relationship to family stress, including crop loss and family illness and injury, is of interest to the growing field of research examining the physiology of parenting. New methods of quantifying male physiological investment using hormonal activity have recently become possible, providing insight into individual-level variation in men's responses to young children [8,13,14]. Relevant studies show that high-investing fathers have lower levels of testosterone than lower-investing fathers [10,14]. However, most of these studies focus on fatherhood during relatively stable environmental conditions, and thus little is known about the physiology of parenthood following a major environmental shock. Several studies have examined associations between cortisol and psychosocial stress following traumatic events [15–17], and while the literature on this theme is still in its infancy, these studies represent an important step toward understanding how shocks such as natural disasters influence human physiology and behavior.

In January and February of 2014, historic floods severely impacted populations residing in lowland Bolivia (Beni Department), including Tsimane Amerindians, who practice a subsistence lifestyle based on horticulture, fishing and hunting [18]. During and immediately following the flood, hundreds of Tsimane families fled to higher ground deep in the forest, or to makeshift encampments in the nearby market town of San Borja (population ~ 25,000). Many homes and possessions in Tsimane villages were abandoned during the rush to escape rising waters of the Maniqui river, which overflowed with little or no warning. Tsimane Health and Life History Project (THLHP) data indicate that > 60 Tsimane villages flooded, with large-scale crop losses affecting nearly all residents. Local media sources, focused their narratives on impacts of flooding among residents of nearby market towns (e.g. San Borja, Rurrenabaque, Yucumo), and reported approximately 60 people and 400,000 livestock were killed, 63,000 ha of crops (e.g. rice, plantain, manioc, corn) were destroyed, and 60,000 families were affected [United Nations [19], International Red Cross [20]]. While smaller scale, localized flooding is common in this tropical region, the 2014 flood was the worst experienced in decades [21] due to recent La Niña and El Niño weather patterns, triggering pervasive food insecurity, disease and injury.

Adverse life events including natural disasters can have profound, long-term hormonal impacts [22] and lasting health consequences [23,24]. While there is a great deal of variation in the type, frequency and severity of adverse life events, human [24], non-human primate [25], and other mammalian models routinely show changes in hypothalamic-pituitary-adrenal (HPA) and hypothalamic-pituitary-gonadal (HPG) activity following a range of adverse life events [24,26]. These impacts often are measured via hormonal dysregulation, either via altered baseline levels, changes in acute hormonal stress responsiveness, or disrupted diurnal variation [16].

This manuscript aims to integrate two parallel literatures; the physiology of parenthood, and hormonal changes following a natural disaster. When disasters occur, they do not just strike single individuals, but disrupt the lives of everyone in a population, especially for families already on the margins of society. Here we examine how disaster impacts the physiology of parental care givers, bridging these two diverse literatures in the context of a major flood.

1.1. Hypotheses

Adverse events can disturb many aspects of physiology, and changes in HPA activity are the most extensively studied [16,22,24]. Many studies report that individuals exposed to major traumatic experiences (e.g. warfare, genocide) who develop post-traumatic stress disorder

(PTSD) show low baseline cortisol levels [15,17,27–29], though see [30]. Psychologically treating PTSD patients with low cortisol levels can increase those levels, suggesting that in some cases cortisol is depressed by repeated stressors or traumatic experiences [31]. The type of stressors, timing of stressor exposure over the life course, intensity and duration of stresses vary across studies, making comparisons difficult [15,30]. In addition, links between cortisol levels and experience of a natural disaster are relatively understudied, especially in populations like the Tsimane who experience various stressors on a daily basis (e.g. high pathogen burden, food insecurity, poverty) [32]. Relevant literature from high income countries (e.g. Japan) indicates that individuals more affected by a major earthquake had lower cortisol [17]. Relatedly, a study of wildfire survivors in Southern California found that individuals with more PTSD symptoms had blunted cortisol [33]. In light of this limited but suggestive evidence, we hypothesize that Tsimane parents who experience greater destructive impacts of flooding, as indicated here by crop losses and threats to family health, will have lower cortisol levels.

In addition to changes in cortisol, we expect severity of the destructive impact of flooding to be associated with lower testosterone, both for physiological and psychosocial reasons. As subsistence horticulturalists, households facing significant crop losses are also likely to experience food insecurity. Psychologically, food insecurity and relative deprivation can be very damaging. From a physiological standpoint, fasting [34], even for short time periods results in immediate decreases in circulating testosterone [35]. In addition to the impacts of food deprivation, illness and injury can downregulate testosterone production [36–38], and immune responses to pathogenic stress are also associated with depressive symptoms [38,39].

From a psychosocial standpoint, when individual and/or group-level status is enhanced (e.g. from winning a competition), testosterone transiently increases in males [40–42] and females [43], and then begins to return to normal levels within an hour [44]. In contrast, testosterone decreases for men who experience even minor losses in athletic or social competition [45–47]. While researchers have not yet examined how long this decline in testosterone lasts following a sports loss, lower levels of testosterone are associated with depressive symptoms in cases of both acute and chronic depressive symptoms [48,49]. While testosterone is associated with many aspects of male biology and psychology such as investment in offspring [8–10,12,14,50], testosterone is not generally associated with maternal behavior in females where other hormones like oxytocin play an important role in mother-infant bonding [7]. In light of this evidence, we expect that men who experience greater destructive impacts of flooding (indicated by crop losses and threats to family health) will have lower levels of testosterone.

2. Methods

2.1. Flood interview and anthropometry

Lowland Bolivian floodwaters peaked in mid-February 2014. As flood waters receded, the THLHP's mobile medical team, with funding from an NSF RAPID grant and private donations to the Tsimane Flood Relief fund, visited 25 Tsimane communities to deliver donations (e.g. horticultural tools) to help people rebuild. After giving donations, mobile team anthropologists conducted interviews regarding crop losses and family health from March 14th–30th, 2014 (eligibility for receiving donations were not contingent on being interviewed). Household heads and/or their spouses reported the total number of tareas (a local measure of area equivalent to 629 m², one-tenth of a hectare) of each of the four staple crops (rice, plantains, manioc and corn) they possessed before the flood, and the total number of tareas that remained viable following flooding. From these data we created two indices: i) absolute number of crops lost across all four staples; and ii) percentage of total tareas of crops lost across all four

staples. For each of the first five co-resident family members, household heads and/or their spouses were systematically asked whether symptoms of illness (e.g. fever, cough, diarrhea, fungus, skin infection) or injury were present (1 = yes, 0 = no) during, or immediately following the flood. These symptoms of illness and injury were chosen because of their conspicuousness and relative ease of identification and reporting. Symptoms were summed and then divided by the number of family members to create two indices i) family disease burden (symptoms per family divided by family members); and ii) child-specific disease burden (symptoms reported for children divided number of children). Indices were separated because total family health (including household head and his/her spouse) can severely impact family production while children's health in particular can substantially increase mortality.

Height was measured with a portable stadiometer (Seca 213), and weight with a digital scale (Tanita BC-1500) for use as control variables.

All participants provided informed consent, and all methods were approved by University of California-Santa Barbara IRB, Tsimane government and village leaders.

2.2. Biomarker collection and analysis

A subset of 421 individuals (mean age = 36.7 years, SD = 13.8, 95% CI = 19.3–64.7 years; 53% male) from 292 households that participated in the flood interview also provided saliva specimens which were later analyzed for cortisol and testosterone. Passive drool saliva was collected following the interview (specimens were collected between 8:55 AM–5:56 PM), and immediately frozen in liquid nitrogen. Specimens were transported on dry ice to the University of California-Santa Barbara Human Biodemography lab. Thirty-four specimens had signs of blood contamination and were excluded from analysis. Saliva was thawed and centrifuged, and the aqueous layer was aliquoted for analysis. Salivary testosterone was measured via enzyme immunoassay (antibody R156/7) [35]. The within and between plate coefficients of variation for testosterone (n = 12 plates) were 7.2% and 7.4% for the low (288.4 pg/mL) and 5.0% and 8.1% for the high (1212.3 pg/mL) controls. Salivary cortisol was measured with enzyme immunoassay (antibody R4866) [35]. The within and between plate coefficients of variation for cortisol (n = 12 plates) were 3.3% and 11.3% for the low (194.5 pg/mL), and 5.6% and 13.4% for the high (969.7 pg/mL) controls.

2.3. Statistical methods

Ordinary Least Squares regression models estimated associations between destructive flood impacts (indices of crop loss and threats to family health) and hormone levels (testosterone and cortisol) for fathers and mothers. Because testosterone and cortisol exhibit strong diurnal variation, time of day is included as a covariate in all regressions. Age and BMI also influence cortisol and testosterone and were included as controls in all regressions. Hormone levels and crop losses (both absolute and proportional) were logged for normality.

3. Results

3.1. Descriptives: crop losses and family health

The average family lost 88% of their total planted crops (median family lost 100%, 95% CI: 18.4%–100%), equivalent to an average of 15.0 tares (95% CI: 1.5–40.3 tares, see Fig. 1). High levels of morbidity were also reported: 81.4% reported that at least one other co-resident household member became ill or injured during or immediately following the flood. The most common reported symptoms were skin fungus (n = 906 cases), cough or fever (n = 414 cases), skin infection (n = 383 cases), diarrhea (n = 365 cases), accident (n = 16

cases). The average family noted 1.57 (\pm 1.3) signs of illness or injury per family member, with each child averaging 1.76 (\pm 1.62) symptoms. Controlling for age and sex, there was no significant association between BMI and proportion of crops lost (Std. β = -0.08 , $p = 0.14$), absolute crop losses (Std. β = 0.05 , $p = 0.34$), or total number of tares of crops saved (Std. β = -0.02 , $p = 0.82$).

3.2. Testosterone but not cortisol is inversely associated with crop losses, particularly for fathers

Controlling for sex, age, BMI, and time of specimen collection, higher proportions of crop losses were associated with lower testosterone (Std. β = -0.14 , $p = 0.020$, see Table 1). The removal of BMI from the model did not substantively alter this association (Std. β = -0.13 , $p = 0.025$). When limited to men only, the association strengthened (Std. β = -0.16 , $p = 0.040$, controlling for age, BMI, time of specimen collection; Fig. 2), while women showed no significant association between testosterone and proportional crop losses (Std. β = -0.13 , $p = 0.177$, same controls). Similarly, greater absolute crop losses were associated with lower male testosterone (Std. β = -0.16 , $p = 0.037$) but not female testosterone (Std. β = -0.03 , $p = 0.778$). Additional models considered associations between testosterone and number of dependent children, and interactions between dependent children and crop losses, but these models provided a poorer fit and these additional covariates were not significant. There was also no association between male testosterone and number of co-resident children controlling for age, time of specimen collection and BMI.

There was no association between cortisol and either proportional or absolute crop loss for males or females.

3.3. Cortisol but not testosterone is inversely associated with family health, particularly for fathers

Higher total family burden of illness and injury (indexed proportional to family size), and child-specific burden (indexed proportional to family size) were associated with lower levels of parental cortisol (Std. β 's = -0.23 and -0.29 respectively, both p 's < 0.001), controlling for age, sex, BMI and time of specimen collection (Tables 2 and 3; Fig. 2). Removing BMI from the models did not alter results (Std. β 's = -0.24 and -0.29 respectively, both p 's < 0.001). When limited to men, the magnitude of the association increased for total family health burden (Std. β = -0.31 , $p < 0.001$), and child-specific burden (Std. β = -0.34 , $p < 0.001$). There was no significant association between female cortisol and total family health burden ($p > 0.1$), but there was a negative association between cortisol and child-specific burden (Std. β = -0.23 , $p = 0.037$, see Tables 2 and 3).

There was no association between male or female testosterone and family or child health burden.

4. Discussion

The 2014 flood had devastating impacts across all 25 surveyed Tsimane communities, with > 98% of individuals reporting flood related crop losses, illness or injury. While nearly all Tsimane were negatively impacted by the flood in some manner, there was a wide range of variation in the level of damage that households faced. We focus on two of the most salient forms of wealth in a subsistence context—food production and health, as both were among the most important forms of human capital throughout history.

The Tsimane have a strong sexual division of labor, with men engaging in the majority of physically intensive horticultural labor [51], while women perform the majority of direct childcare [52]. To lose a field after clearing trees, burning the field, planting and weeding results in a significant (roughly a year's worth) loss of labor and food. Horticultural products comprise 66% of the Tsimane diet [53], so major horticultural losses severely impact familial well-being. As predicted,

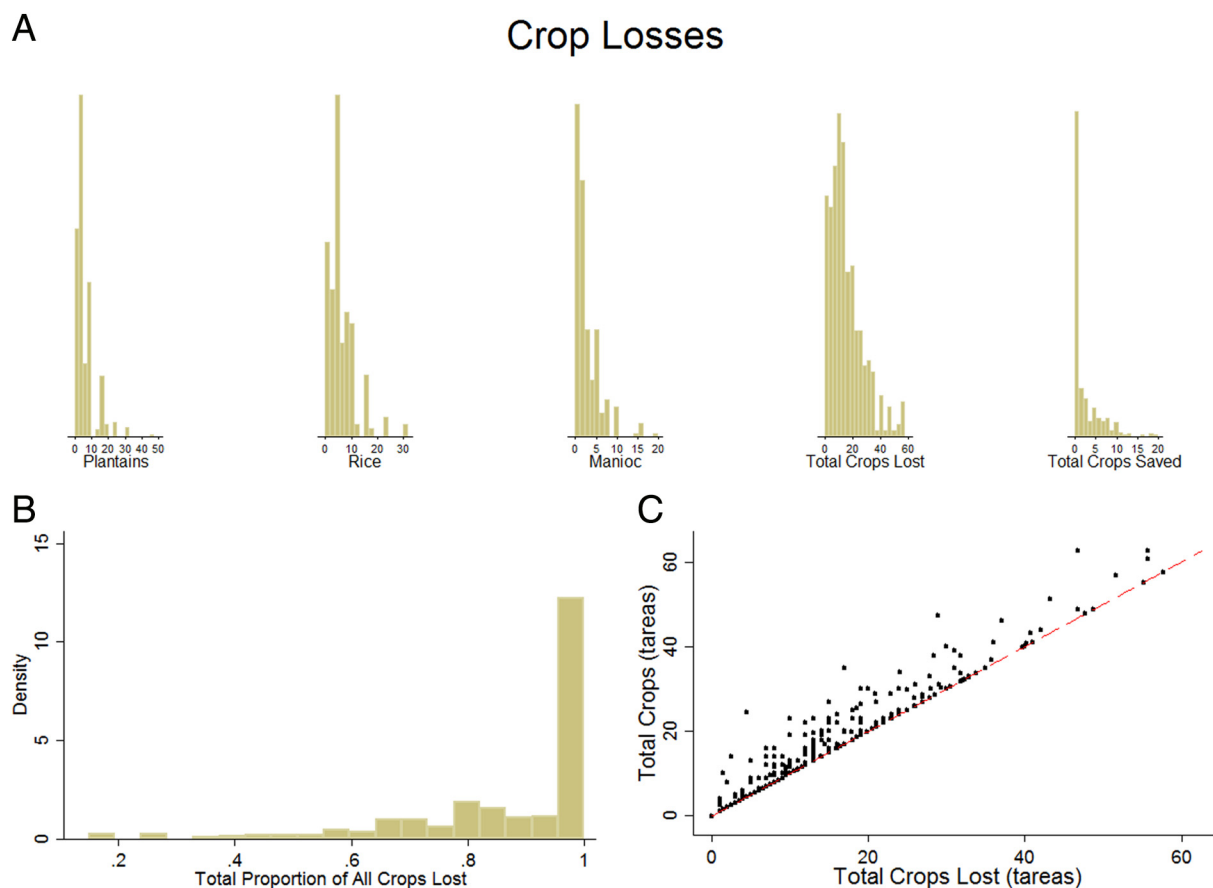


Fig. 1. A) absolute (in tares) crop losses, B) proportion of total crops lost, and C) total crops and crop losses with 100% of all crops lost indicated by the red dotted line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Associations between proportion of total crops lost and log testosterone (OLS regression models), controlling for sex, time of saliva collection, age, and BMI.

	All participants (n = 317)		Males only (n = 176)		Females only (n = 143)	
	Std β	P	Std β	P	Std β	P
Proportional crop loss (log)	-0.136	0.020	-0.157	0.040	-0.132	0.177
Male gender	0.236	< 0.001				
Time of saliva collection	0.098	0.095	0.106	0.165	0.102	0.297
Age (years)	-0.107	0.072	-0.183	0.020	-0.012	0.905
BMI	-0.075	0.202	-0.071	0.361	-0.062	0.527
AIC	343.94		190.61		157.42	

men with greater crop losses had lower levels of salivary testosterone than men with fewer crop losses. In industrialized populations male depression is associated with low levels of testosterone [48,49], and even acute depressive events show decreases in testosterone [45,47]. Additionally, reduced caloric intake and illness also cause decreases in testosterone [35,36], so it is perhaps unsurprising that when a major environmental shock such as flooding causes crop loss, men exhibit a decrease in testosterone. Men reporting personal morbidity (illness or injury) did not have significantly lower testosterone, suggesting that the associations between testosterone and crop losses were not due to illness.

There was no association between female testosterone and flood-induced crop loss. Tsimane women engage in horticultural activity (e.g. weeding fields, harvesting), and while crop loss may be a salient category that resulted in major psychosocial distress and loss of food, it does not manifest in lower levels of testosterone. Alternatively, crop losses may not cause as much direct psychological distress to women, as intensive horticultural labor is perceived largely as the domain of men's

work. Future studies will examine psychological distress and depressive and anxious affect in association with crop and other losses resulting from the flood.

Low baseline cortisol following a prolonged major stress event, or series of events, has been reported previously following a natural disaster [17], and in some but not all cases of PTSD [15,16,27–30,54]. There are biologically plausible reasons why sustained HPA hyperactivity from repeated stressors can result in long-term downregulation of cortisol, but the lack of longitudinal or experimental studies precludes stronger inferences [16,54]. One possible mechanism linking PTSD and HPA disruption is via changes in sleeping patterns, which are a common symptom of PTSD [55–57]. In this study, we asked participants if they had experienced changes in sleep (73.6% of this sample reported changes in sleep patterns during/after the flood), but unfortunately did not collect data on whether sleep increased or decreased. Thus, sleep disruptions could be another possible explanation for why fathers who lost more crops had lower testosterone, and parents with a greater family burden of health issues showed lower

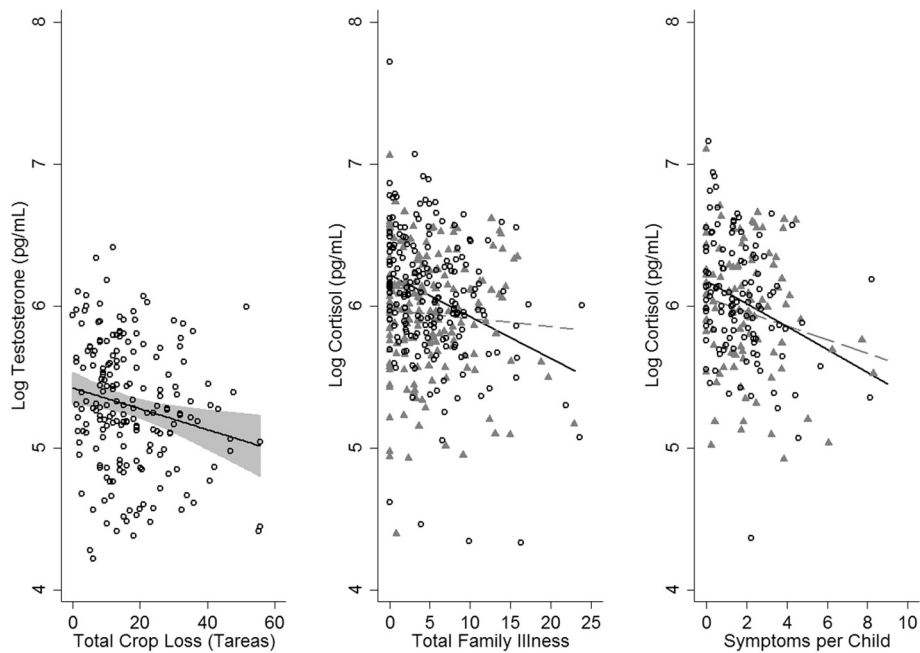


Fig. 2. Associations between hormones and flood-related crop loss and illness. Males are indicated by open circles and solid lines, females indicated by filled triangles and dashed lines.

cortisol.

Tsimane men with a higher total burden of family and child health problems showed lower cortisol levels. While Tsimane men only spend 4.5% of their waking time in direct childcare of young children (compared to 31.6% for mothers) [52], it is clear that paternal investments (e.g. food production, information transmission) are important in children's lives. Previous analyses indicate that odds of a Tsimane child dying before the age of four are nearly three times higher if their father dies [58]. While men may not engage in high levels of direct childcare, in the context of modernization, men are more likely to speak Spanish than women and thus are more likely to seek and procure modern medicine for sick children in the nearby market town. As with fathers, we found a negative association between child health burden and maternal cortisol. Given their substantial time allocation to providing direct childcare, mothers are likely the first to notice acute health problems in children.

4.1. Comparison to other natural disasters

While data are limited, several studies report the impact of natural disasters on health. In the Philippines, doctor consultations increased following natural disasters including floods, earthquakes and typhoons [59], especially for acute respiratory infections. While our data are not directly comparable because we did not examine people seeking treatment, fungal infections and respiratory infections were the most common symptoms reported. Following other natural disasters such as a major earthquake in Peru, infections rapidly spread [60], and while

more detailed health data were not collected in this study, it seems likely that there was an increase in exposure to many types of pathogens due to wells and latrines being inundated, and long standing still water.

Even in industrialized populations, which generally have insurance companies, disaster relief infrastructure, relative food security and reliable medical care, and other social security mechanisms, there is evidence that natural disasters are associated with blunted diurnal cortisol variability [33]. While data in the present study are limited to a relatively short period directly following the flood, longer term studies in the US find that maternal stress following flooding predicts toddler cortisol reactivity years later [61]. Similarly, lasting changes in mental health were reported following the 2004 Indian Ocean Tsunami [62].

4.2. Limitations

As the current study was survey-based and designed to interview large portions of the population in a relatively short period, it was not possible to directly assess nutritional intake; anthropometric assessment unfortunately does not allow us to measure changes in food availability pre- versus post-flood. Thus, declines in male testosterone could have partially resulted from acute changes in food availability. Similarly, acute illness can result in declines in testosterone [36–38], and while we did not see evidence that males reporting illness had lower testosterone, it should be noted that data was collected after flood waters receded. Thus if men were ill during the peak of the flood they may have experienced acute decreases in testosterone at that time, but not at

Table 2

Associations between family burden of illness and log cortisol (OLS regression models), controlling for sex, time of saliva collection, age, and BMI.

	All participants (n = 310)		Males only (n = 171)		Females only (n = 139)	
	Std β	P	Std β	P	Std β	P
Total family burden of illness and injury	-0.232	< 0.001	-0.311	< 0.001	-0.134	0.113
Male gender	0.125	0.023				
Time of saliva collection	-0.007	0.901	0.043	0.559	-0.063	0.454
Age (years)	0.005	0.929	0.031	0.681	-0.021	0.808
BMI	-0.164	0.003	-0.161	0.034	-0.190	0.029
AIC	349.65		191.62		163.32	

Table 3

Associations between co-resident children's health problems and log cortisol (OLS regression models), controlling for sex, time of saliva collection, age, and BMI.

	All participants (n = 187)		Males only (n = 106)		Females only (n = 81)	
	Std β	P	Std β	P	Std β	P
Total child burden of illness and injury	–0.290	< 0.001	–0.341	< 0.001	–0.231	0.037
Male gender	0.056	0.437				
Time of saliva collection	0.003	0.967	0.003	0.972	–0.001	0.992
Age (years)	–0.078	0.268	–0.071	0.454	–0.089	0.416
BMI	–0.181	0.011	–0.150	0.117	–0.220	0.046
AIC	204.39		107.45		102.82	

the time specimens were collected.

This is an observational and cross-sectional study, and thus cannot assess causality. Studies following personal, local, or large-scale disasters are difficult to conduct as such disasters often occur without warning, especially in remote regions. While an ideal study design would involve pre-and post-flood hormonal and health data, saliva is not routinely collected as part of the THLHP [18], and thus there were no comparable baseline salivary data to compare hormone levels before and after the flood.

Many studies find a stronger association between chronic stress and abnormal diurnal variation in cortisol, rather than single point cortisol measures (e.g. [28]). Collection of repeated saliva measurements per person throughout the day would have been an ideal study design, but unfortunately we were limited by the need to collect data quickly immediately following the flood.

Another study limitation is that because some crop types are more energetically productive per unit of area (e.g. rice can produce more calories per hectare than plantain), a sum of all crop losses may not reflect total calories or time lost. However, labor costs vary for different crops, as do micronutrient contents, amino acids and protein levels, so by combining all crop types we can get an overall estimate of loss. Similarly, some types of illness or injury are costlier than others, and thus a sum of all illnesses and injuries may not accurately reflect severity of family health burden. That said, these were self-reported symptoms, not symptoms clinically assessed by a physician, so we felt that a sum of symptoms was better for establishing overall health burden than attempting to apply severity of illness or injury.

Menstrual cycle data were not collected for women, nor was lactation status. While inter-individual and diurnal fluctuation in testosterone is greater than menstrual cycle variation in hormones [63], this limitation does minimize the utility of our female testosterone data.

While crop losses and child illness are two of the most salient and potentially life threatening losses that occurred during the flood, material possessions and domesticated animals (e.g. pigs, dogs) were also lost by Tsimane due to flooding. Future studies will examine how other types of losses (e.g. material possessions, money, debts incurred during the flood) impact family health and well-being; follow-up studies will examine which strategies resulted in faster rebound and rebuilding following flooding.

4.3. Conclusions

Fathers provide critical investments, including food, protection, instruction and direct care. Comparing relative impacts of different types of paternal investments and measuring hormonal correlates of paternal investment is a growing area of research [9,10,12,14]. Following a major 2014 flood, we find that greater crop losses are associated with lower levels of male testosterone, consistent with parallel literatures addressing physiology of the stress response and parenting. Crop losses were not associated with female hormonal levels. Men who experienced a higher proportion of familial and child-specific illness and injury had lower levels of cortisol. These results highlight the physiological and psychosocial costs of a natural disaster, especially for

fathers in a high fertility, nutritionally and pathogenically stressed subsistence population where horticultural labor provides the majority of calories in the diet.

Acknowledgements

We thank THLHP personnel and staff for their dedicated wide-ranging efforts toward community-based participatory research. We thank the National Science Foundation (NSF) and National Institutes of Health/National Institute on Aging (NIH/NIA) for financial support (RAPID BCS-1440212; R01AG024119, R56AG024119). Lisa McAllister and Melanie Martin helped establish the Tsimane Flood Relief Fund that enabled THLHP to increase aid. JS acknowledges financial support from the Agence Nationale de la Recherche (ANR) – Labex IAST.

References

- [1] J. Leaning, D. Guha-Sapir, Natural disasters, armed conflict, and public health, *N. Engl. J. Med.* 369 (2013) 1836–1842.
- [2] S.C. Antón, R. Potts, L.C. Aiello, Evolution of early homo: an integrated biological perspective, *Science* 345 (2014).
- [3] B. Winterhalder, Diet choice, risk, and food sharing in a stochastic environment, *J. Anthropol. Archaeol.* 5 (1986) 369–392.
- [4] H. Kaplan, K. Hill, J. Lancaster, A. Hurtado, A theory of human life history evolution: diet, intelligence, and longevity, *Evol. Anthropol.* 9 (2000) 156–185.
- [5] P.L. Hooper, M. Gurven, J. Winking, H.S. Kaplan, Inclusive fitness and differential productivity across the life course determine intergenerational transfers in a small-scale human society, *Proc. R. Soc. Lond. B Biol. Sci.* 282 (2015) 20142808.
- [6] R. Bliege Bird, D.W. Bird, E.A. Smith, G.C. Kushnick, Risk and reciprocity in Meriam food sharing, *Evol. Hum. Behav.* 23 (2002) 297–321.
- [7] B.C. Trumble, A.V. Jaeggi, M. Gurven, Evolving the neuroendocrine physiology of human and primate cooperation and collective action, *Philos. Trans. R. Soc. B* 370 (2015) 20150014.
- [8] L.T. Gettler, Applying socioendocrinology to evolutionary models: fatherhood and physiology, *Evol. Anthropol.* 23 (2014) 146–160.
- [9] L.T. Gettler, T.W. McDade, S.S. Agustin, A.B. Feranil, C.W. Kuzawa, Longitudinal perspectives on fathers' residence status, time allocation, and testosterone in the Philippines, *Adapt. Hum. Behav. Physiol.* 1 (2015) 124–149.
- [10] P.B. Gray, S.M. Kahlenberg, E.S. Barrett, S.F. Lipson, P.T. Ellison, Marriage and fatherhood are associated with lower testosterone in males, *Evol. Hum. Behav.* 23 (2002) 193–201.
- [11] S. Tecot, A. Baden, Profiling caregivers: hormonal variation underlying allomaternal care in wild red-bellied lemurs, *Eulemur rubriventer*, *Physiol. Behav.* (2018).
- [12] S. Rosenbaum, L.T. Gettler, With a little help from her friends (and family) part II: non-maternal caregiving behavior and physiology in mammals, *Physiol. Behav.* (2018).
- [13] L. Ting, J. Mascaro, K. Bijanki, L. Arnal, M. Adams, R. Barr, et al., Explaining individual variation in paternal brain responses to infant cries, *Physiol. Behav.* (2018).
- [14] M.S. Sarma, P.X. Kou, S.A. Bechayda, C.W. Kuzawa, L.T. Gettler, Exploring the links between early life and young adulthood social experiences and men's later life psychobiology as fathers, *Physiol. Behav.* (2018).
- [15] R. Yehuda, Post-traumatic stress disorder, *N. Engl. J. Med.* 346 (2002) 108–114.
- [16] R. Yehuda, E.L. Giller, S.M. Southwick, M.T. Lowy, J.W. Mason, Hypothalamic-pituitary-adrenal dysfunction in posttraumatic stress disorder, *Biol. Psychiatry* 30 (1991) 1031–1048.
- [17] T. Yonekura, K. Takeda, V. Shetty, M. Yamaguchi, Relationship between salivary cortisol and depression in adolescent survivors of a major natural disaster, *J. Physiol. Sci.* 64 (2014) 261–267.
- [18] M. Gurven, J. Stieglitz, B.C. Trumble, A.D. Blackwell, B. Beheim, H. Davis, et al., The Tsimane Health and Life History Project: integrating anthropology and biomedicine, *Evol. Anthropol.* 26 (2) (2017) 54–73.
- [19] U. Nations, Bolivia: Emergencia Inundaciones, (2014), p. 2014.
- [20] I.R. Cross, Emergency Plan of Action Bolivia Floods, International Federation of Red

- Cross and Red Crescent, 2014.
- [21] UNISDR, Americas hit hard by El Nino, United Nations Office for Disaster Risk Reduction Regional Office for the Americas, UNISDR AM, 2015.
- [22] B.S. McEwen, Brain on stress: how the social environment gets under the skin, *Proc. Natl. Acad. Sci.* 109 (2012) 17180–17185.
- [23] Z. Thayer, C. Barbosa-Leiker, M. McDonell, L. Nelson, D. Buchwald, S. Manson, Early life trauma, post-traumatic stress disorder, and allostatic load in a sample of American Indian adults, *Am. J. Hum. Biol.* 29 (2017) (e22943-n/a).
- [24] G.P. Chrousos, P.W. Gold, The concepts of stress and stress system disorders: overview of physical and behavioral homeostasis, *JAMA* 267 (1992) 1244–1252.
- [25] K.A. O'Connor, E. Brindle, J. Shofer, B.C. Trumble, J.D. Aranda, K. Rice, et al., The effects of a long-term psychosocial stress on reproductive indicators in the baboon, *Am. J. Phys. Anthropol.* 145 (2011) 629–638.
- [26] D.J. Newport, Z.N. Stowe, C.B. Nemeroff, Parental depression: animal models of an adverse life event, *Am. J. Psychiatr.* 159 (2002) 1265–1283.
- [27] R. Yehuda, S.M. Southwick, G. Nussbaum, V. Wahby, E.L. GILLER Jr, J.W. Mason, Low urinary cortisol excretion in patients with posttraumatic stress disorder, *J. Nerv. Ment. Dis.* 178 (1990) 366–369.
- [28] R. Yehuda, M.H. Teicher, R.L. Trestman, R.A. Levengood, L.J. Siever, Cortisol regulation in posttraumatic stress disorder and major depression: a chronobiological analysis, *Biol. Psychiatry* 40 (1996) 79–88.
- [29] J.W. Mason, E.L. Giller, T.R. Kosten, R.B. Ostroff, L. Podd, Urinary free-cortisol levels in posttraumatic stress disorder patients, *J. Nerv. Ment. Dis.* 174 (1986) 145–149.
- [30] M.-L. Meewisse, J.B. Reitsma, G.-J. De Vries, B.P.R. Gersons, M. Olff, Cortisol and post-traumatic stress disorder in adults, *Syst. Rev. Meta Anal.* 191 (2007) 387–392.
- [31] M. Olff, G.-J. de Vries, Y. Güzelcan, J. Assies, B.P. Gersons, Changes in cortisol and DHEA plasma levels after psychotherapy for PTSD, *Psychoneuroendocrinology* 32 (2007) 619–626.
- [32] J. Stieglitz, A.V. Jaeggi, A.D. Blackwell, B.C. Trumble, M. Gurven, H. Kaplan, Work to Live and Live to Work: Productivity, Transfers, and Psychological Well-Being in Adulthood and Old Age, (2014).
- [33] D.J. Thompson, I. Weissbecker, E. Cash, D.M. Simpson, M. Daup, S.E. Sephton, Stress and cortisol in disaster evacuees: an exploratory study on associations with social protective factors, *Appl. Psychophysiol. Biofeedback* 40 (2015) 33–44.
- [34] J.L. Cameron, T.E. Weltzin, C. McConaha, D.L. Helmreich, W.H. Kaye, Slowing of pulsatile luteinizing hormone secretion in men after forty-eight hours of fasting, *J. Clin. Endocrinol. Metab.* 73 (1991) 35–41.
- [35] B.C. Trumble, E. Brindle, M. Kupsik, K.A. O'Connor, Responsiveness of the reproductive axis to a single missed evening meal in young adult males, *Am. J. Hum. Biol.* 22 (2010) 775–781.
- [36] D.I. Spratt, P. Cox, J. Orav, J. Moloney, T. Bigos, Reproductive axis suppression in acute illness is related to disease severity, *J. Clin. Endocrinol. Metab.* 76 (1993) 1548–1554.
- [37] Z.L. Simmons, J.R. Roney, Androgens and energy allocation: quasi-experimental evidence for effects of influenza vaccination on men's testosterone, *Am. J. Hum. Biol.* 21 (2009) 133–135.
- [38] E.C. Shattuck, M.P. Muehlenbein, Human sickness behavior: ultimate and proximate explanations, *Am. J. Phys. Anthropol.* 157 (2015) 1–18.
- [39] J. Stieglitz, B.C. Trumble, M.E. Thompson, A.D. Blackwell, H. Kaplan, M. Gurven, Depression as sickness behavior? A test of the host defense hypothesis in a high pathogen population, *Brain Behav. Immun.* 49 (2015) 130–139.
- [40] J. Archer, Testosterone and human aggression: an evaluation of the challenge hypothesis, *Neurosci. Biobehav. Rev.* 30 (2006) 319–345.
- [41] K.V. Casto, D.A. Edwards, Testosterone, cortisol, and human competition, *Horm. Behav.* 82 (2016) 21–37.
- [42] S.N. Geniole, B.M. Bird, E.L. Ruddick, J.M. Carré, Effects of competition outcome on testosterone concentrations in humans: an updated meta-analysis, *Horm. Behav.* 92 (2017) 37–50.
- [43] T. Oliveira, M. Gouveia, R.F. Oliveira, Testosterone responsiveness to winning and losing experiences in female soccer players, *Psychoneuroendocrinology* 34 (2009) 1056–1064.
- [44] B.C. Trumble, D. Cummings, C. von Rueden, K.A. O'Connor, E.A. Smith, M. Gurven, et al., Physical competition increases testosterone among Amazonian forager-horticulturalists: a test of the 'challenge hypothesis', *Proc. R. Soc. B Biol. Sci.* 279 (1739) (2012) 2907–2912.
- [45] P.C. Bernhardt, J.M. Dabbs Jr., J.A. Fielden, C.D. Lutter, Testosterone changes during vicarious experiences of winning and losing among fans at sporting events, *Physiol. Behav.* 65 (1998) 59–62.
- [46] S.J. Stanton, J.C. Beehner, E.K. Saini, C.M. Kuhn, K.S. Labar, Dominance, politics, and physiology: voters' testosterone changes on the night of the 2008 United States presidential election, *PLoS One* 4 (2009) e7543.
- [47] M. Jiménez, R. Aguilar, J.R. Alvero-Cruz, Effects of victory and defeat on testosterone and cortisol response to competition: evidence for same response patterns in men and women, *Psychoneuroendocrinology* 37 (2012) 1577–1581.
- [48] M.M. Shores, V.M. Mocerri, K.L. Sloan, A.M. Matsumoto, D.R. Kivlahan, Low testosterone levels predict incident depressive illness in older men: effects of age and medical morbidity, *J. Clin. Psychiatry* 66 (2005) 7–14.
- [49] A.H. Ford, B.B. Yeap, L. Flicker, G.J. Hankey, S.A.P. Chubb, D.J. Handelsman, et al., Prospective longitudinal study of testosterone and incident depression in older men: the health in men study, *Psychoneuroendocrinology* 64 (2016) 57–65.
- [50] P.B. Gray, T.S. McHale, J.M. Carré, A review of human male field studies of hormones and behavioral reproductive effort, *Horm. Behav.* 91 (2017) 52–67.
- [51] B.C. Trumble, D.K. Cummings, K.A. O'Connor, D.J. Holman, E.A. Smith, H.S. Kaplan, et al., Age-independent increases in male salivary testosterone during horticultural activity among Tsimane forager-farmers, *Evol. Hum. Behav.* 34 (2013) 350–357.
- [52] J. Winking, M. Gurven, H. Kaplan, J. Stieglitz, The goals of direct paternal care among a South Amerindian population, *Am. J. Phys. Anthropol.* 139 (2009) 295–304.
- [53] M.A. Martin, W.D. Lassek, S.J.C. Gaulin, R.W. Evans, J.G. Woo, S.R. Geraghty, et al., Fatty acid composition in the mature milk of Bolivian forager-horticulturalists: controlled comparisons with a US sample, *Matern. Child Nutr.* 8 (2012) 404–418.
- [54] R. Yehuda, J. Seckl, Minireview: stress-related psychiatric disorders with low cortisol levels: a metabolic hypothesis, *Endocrinology* 152 (2011) 4496–4503.
- [55] K.P. Wright, A.L. Drake, D.J. Frey, M. Fleshner, C.A. Desouza, C. Gronfier, et al., Influence of sleep deprivation and circadian misalignment on cortisol, inflammatory markers, and cytokine balance, *Brain Behav. Immun.* 47 (2015) 24–34.
- [56] B.S. McEwen, I.N. Karatsoreos, Sleep deprivation and circadian disruption, *Sleep Med. Clin.* 10 (2015) 1–10.
- [57] A. Germain, Sleep disturbances as the hallmark of PTSD: where are we now? *Am. J. Psychiatr.* 170 (2013) 372–382.
- [58] J. Winking, M. Gurven, H. Kaplan, The impact of parents and self-selection on child survival among the Tsimane of Bolivia, *Curr. Anthropol.* 52 (2011) 277–284.
- [59] M.A. Salazar, A. Pesigan, R. Law, V. Winkler, Post-disaster health impact of natural hazards in the Philippines in 2013, *Glob. Health Action* 9 (2016) 31320.
- [60] D. Vasquez, A. Palacio, J. Nuñez, W. Briones, J.C. Beier, D.C. Pareja, et al., Impact of the 2016 Ecuador earthquake on Zika virus cases, *Am. J. Public Health* 107 (2017) 1137–1142.
- [61] E. Yong Ping, D.P. Laplante, G. Elgbeili, K.M. Hillerger, A. Brunet, M.W. O'Hara, et al., Prenatal maternal stress predicts stress reactivity at 2½ years of age: the Iowa Flood Study, *Psychoneuroendocrinology* 56 (2015) 62–78.
- [62] E. Frankenberg, J. Friedman, T. Gillespie, N. Ingwersen, R. Pynoos, I.U. Rifai, et al., Mental health in Sumatra after the tsunami, *Am. J. Public Health* 98 (2008) 1671–1677.
- [63] J.M. Dabbs Jr., D. de La Rue, Salivary testosterone measurements among women: relative magnitude of circadian and menstrual cycles, *Horm. Res. Paediatr.* 35 (1991) 182–184.