Food Aversions and Cravings during Pregnancy on Yasawa Island, Fiji

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Abstract

PURPOSE: Women often experience novel food aversions and cravings during pregnancy. These appetite changes have been hypothesized to represent adaptive responses to challenges posed by pregnancy, including maternal immune suppression, metabolic changes, and oxidative stress and fetal organogenesis and growth requirements. Here, we assess the extent to which data from an indigenous population in Fiji accord with predictions of this hypothesis.

METHODS: We use interview data from 70 Fijian women from Yasawa Island to qualitatively assess the predictions that aversions focus preferentially on foods likely to aggravate the challenges of pregnancy and that cravings focus preferentially on foods containing nutrients likely to be depleted by these challenges. We also use the χ^2 test to quantitatively test the prediction that women experiencing nutrient losses due to aversions are more likely than other women to crave foods containing missing nutrients.

RESULTS: Aversions focus predominantly on foods expected to exacerbate the challenges of pregnancy such as fish and cassava. Cravings usually focus on bananas/plantains, fruits, and other foods that provide calories and micronutrients while posing few threats to mothers and fetuses. Women that experience aversions to specific foods are more likely than other women to crave foods that meet similar nutritional needs as those provided by the aversive foods.

CONCLUSIONS: Our data support the hypothesis that food aversions and cravings experienced by many pregnant women reflect adaptive responses to challenges of pregnancy. The aversions and cravings may operate in tandem with culturally transmitted information that also offers pregnant women adaptive guidance regarding diet.

1. Introduction

In this paper, we report new evidence regarding appetite changes during pregnancy in an indigenous population from Yasawa Island, Fiji. In particular, we focus on the development of aversions to foods that the women usually like but found unpalatable during pregnancy as well as on the development of strong, specific cravings for foods during pregnancy. The patterning in the aversions and cravings data from the Yasawa women is consistent with the hypothesis that appetite changes in pregnancy are an adaptive strategy for dealing with challenges to maternal and offspring fitness posed by gestation.

Relative to other life stages, pregnancy presents a major opportunity for selective processes to operate on both genes and culture in humans (Brown et al. 2013). For mothers and offspring, pregnancy poses at least five unique immunological, endocrinological, metabolic, and developmental challenges. These five challenges of pregnancy are: adaptive immune suppression, embryo tissue differentiation, genetic conflict, oxidative stress, and changes in energy budget. We describe these challenges in detail below:

1) **Adaptive Immune-Suppression:** To facilitate the tolerance of non-self fetal tissue, mothers down-regulate their own immune functions following conception. This immune system suppression leaves mothers and embryos particularly vulnerable to exploitation by pathogens (Flaxman & Sherman 2000; Fessler 2002a; Svensson-Arvelund et al. 2013).
2) **Embryo Tissue Differentiation:** Embryonic tissues differentiate and organogenesis occurs in early pregnancy. Developmental insults due to illness or exposure to chemical toxins during this phase can have particularly radical downstream negative effects on offspring phenotype (Langley-Evans 2006; Myatt 2006; Rillamas-Sun 2010).
3) **Genetic Conflict:** Pregnancy requires mother and offspring to share maternal resources, but offspring interests usually differ from those of their mothers because they have only ~50% of their genes in common (Trivers 1974; Haig 1993). As such, offspring generally demand more energetic investment than mothers are willing to supply. This genetic conflict can negatively impact maternal metabolic function and offspring health and survivorship if the result favours either the mother or the offspring rather than equitably partitioning resources (Haig 1993; Crespi & Badcock 2008; Das et al. 2009; Crespi 2010; 2011). Unchecked fetal manipulation of maternal endocrinology can dangerously elevate maternal blood pressure and

rates of protein excretion (preeclampsia) and/or impair sugar absorption and elevate circulating sugar levels (gestational diabetes mellitus).

4) **Oxidative Stress:** Normal cell metabolism produces reactive oxygen-based molecules ("reactive oxygen species") that can cause cell damage and DNA degradation. Presence of antioxidants (compounds that neutralize reactive oxygen species so that they can be safely excreted) limits the toxicity of such molecules. However, placental tissues produce particularly high volumes of reactive oxygen species, often to the extent that they outnumber stored or normal dietary antioxidants, resulting in oxidative stress. Oxidative stress in pregnancy is associated with several negative health and survivorship outcomes for both mothers and offspring including egg cell degradation, degradation of the uterine lining, increased risk of spontaneous abortion, preeclampsia, and fetal growth restriction (Jauniaux et al. 2006; Al-Gubory 2013; Paine et al. 2013).
5) **Changes in Energy Budget:** Support of a fetus increases a mother's energy and nutrient requirements (Dufour & Sauther 2002; Fessler 2002a). Intake requirements increase during or immediately following a time in which maternal diet is often circumscribed by nausea, vomiting, and the development of novel aversions to foods, making it more difficult for pregnant women relative to other adults to secure and mobilize needed energy and nutrients.

All of these pregnancy challenges affect and/or are affected by diet and eating behaviours. At the same time, eating presents its own set of adaptive challenges throughout the lifecourse for both males and females (Sherman & Flaxman 2001). Many edible compounds necessary for growth, development, and body maintenance can result in toxicity or poisoning if ingested at rates above a size-specific and development-stage-specific dose threshold (Gerber et al. 1999). Furthermore, most plant-based foods have evolved to produce toxic compounds to reduce the risk of exploitation by fungi, parasites, pathogens, and invertebrate and vertebrate predators (Billing & Sherman 1998; Flaxman & Sherman 2000; Sherman & Hash 2001; Sherman & Flaxman 2001; Fessler 2002a; Flaxman & Sherman 2008). Such compounds can disrupt or even shut down cellular function in humans. Lastly, eating provides food-borne pathogens ready access to the bloodstream (Sherman & Flaxman 2001).

Evidence suggests that humans have evolved a number of physiological, psychological and cultural solutions to the challenges associated with eating (Eaton & Konner 1985; Patil & Young 2012). With respect to physiology, ingestion of biochemical toxins and/or high levels of food-borne pathogens can trigger a number of symptoms, most notably vomiting and diarrhea, which facilitate the rapid expulsion of toxic or contaminated food items (Flaxman & Sherman 2000). Psychologically, we experience appetite sensations such as the development of aversions to foods previously associated with physiologic expressions

of nausea, vomiting, or diarrhea and the development of cravings for foods that contain difficult-to-obtain nutrients (Williams & Nesse 1991; Patil & Young 2012). Such aversions and cravings appear to be associated with, respectively, motivations to avoid or motivations to seek particular foodstuffs (Drewnowski 1997; Sclafani 1997). Culturally, many human populations possess food taboos – prohibitions against eating certain foods – that appear to focus preferentially on foods especially likely to pose health risks (Fessler & Navarrete 2003). Moreover, many populations have developed food preparation techniques that involve heating foods to temperatures sufficiently high to denature bacterial proteins and/or adding spices that contain antimicrobial compounds at levels sufficient to slow the proliferation of food-borne pathogens (Billing & Sherman 1998; Sherman & Flaxman 2001; Sherman & Hash 2001). Also in the cultural realm, in many populations, particular food items and recipes are associated with desirability, and such food items frequently contain difficult-to-access essential nutrients (Rozin & Vollmecke 1986).

Given that selection is strong during pregnancy and that human diet generally appears to have been shaped by both genetic and cultural evolution to adaptively reduce exposure to food-borne pathogens and toxins and to increase procurement of essential nutrients, we should expect humans to have developed specific dietary adaptations in relation to the unique challenges of pregnancy.

A number of hypotheses have been put forward in the literature that propose functional and evolutionary links between pregnancy-related changes in visceral appetite sensations (food aversions and cravings not mediated by conscious, rational thought) and one or more of the challenges associated with pregnancy. These hypotheses, their main predictions, and to which challenges of pregnancy they relate are summarized in Table 1 as well as described in the text that follows.

[Table 1]

The **maternal-embryo protection hypothesis** holds that the development of novel food aversions during pregnancy reflects a set of evolved mechanisms that motivate women to avoid foods that are especially likely to contain pathogenic and chemical toxins during maternal adaptive immune suppression and during embryo tissue differentiation (see also Hook 1978; 1980; 1988; Profet 1992; 1997; Flaxman & Sherman 2000; Fessler 2002). According to Fessler (2002), this phenomenon may extend beyond visceral aversions, such that culturally evolved food taboos also function to reduce maternal and embryo exposure to toxins during the vulnerable developmental window.

The **compensatory placental growth hypothesis** proposes that pregnancy-related food aversions result from fetal manipulation of maternal physiology that motivates mothers to avoid energy-dense foods. Counter-intuitively, maternal energy restriction benefits fetuses

because energy-restricted mothers prioritize allocating whatever resources they have available to embryo and placental development (Huxley 2000).

Brown et al. (2013) outline a hypothesis that we call the **gestational metabolic syndrome avoidance hypothesis**. This hypothesis holds that food aversions during pregnancy may have evolved in part to motivate women to avoid eating foods that increase the risk of developing gestational diabetes mellitus and preeclampsia. These two pregnancy complications appear to represent extreme, pathological expressions of genetic conflict in which fetuses promote placental artery restriction and inhibit maternal sugar absorption so as to secure relatively high levels of maternal investment (Haig 1993; Haig 1999). But, according to the hypothesis, mothers may also have evolved various counter-adaptations to reduce the risk of developing these pathologies.

The **nutrient-seeking hypothesis** proposes that pregnancy-related cravings motivate women to find and eat foods containing energy, macro-, and micro- nutrients essential to fetal development (Hook 1978; 1980; Tierson et al. 1985). Fessler (2002) suggests an important addendum to this hypothesis: pregnant women may have particular propensities to seek nutrients that are depleted in or missing from their diets due to food aversions and vomiting.

Lastly, we propose the **antioxidant procurement hypothesis**. According to this hypothesis, some pregnancy-related cravings represent evolved motivations to consume foods that contain high levels of antioxidants so as to mitigate the effects of oxidative stress related to placentation and placental maintenance. Consumption of foods containing large quantities of antioxidants such as most fruits and greens increases the availability of antioxidants to bind with and neutralize reactive oxygen species that would otherwise disrupt or damage cellular function in pregnant women and fetuses.

Each of these hypotheses has some empirical support, although few formal tests have been carried out to date. Data from a number of studies regarding within or among population variation in diet composition and expression of food aversions in pregnancy are consistent with the maternal-embryo protection hypothesis. The data in question suggest that such aversions focus preferentially on animal foods – which are subject to high rates of spoilage if refrigeration is not available, especially in hot climates – and/or on plant foods that are high in toxins (Flaxman & Sherman 2000; Fessler 2002a; Pepper & Roberts 2006; Weigel et al. 2011; Steinmetz et al. 2012; Mckerracher et al. 2014). Evidence from a cross-national study carried out by Pepper and Roberts (2006) is consistent with the compensatory placental growth hypothesis. These authors found that women are more likely to develop nausea during pregnancy in countries with more nutrient dense diets. Additionally, a veterinary medicine study published in 1998 found that sheep fed more restricted diets

produced offspring with larger placentas, seemingly favouring early fetal growth (Lunney 1998). Regarding the gestational metabolic syndrome avoidance hypothesis, evidence from more than one million births in New York between 1995 and 2003 suggests that women from populations with long histories of farming are less likely to develop gestational diabetes mellitus (Savitz et al. 2008), perhaps indicating the evolution of a maternal counter-adaptation to fetal energy demands in environmental contexts in which calories are abundant (Brown et al. 2013). In addition, some recent studies on populations without long histories of farming have found that, in such populations, women frequently find starchy cereal crops aversive. The nutrient-seeking hypothesis is supported by several studies that suggest the most aversive foods are also the least likely to be craved and vice versa (e.g. Flaxman & Sherman 2000; Weigel et al. 2011; Steinmetz et al. 2012). This pattern may be consistent with the view that women have evolved a pregnancy-specific mechanism to seek out sources of energy and possibly other nutrients when they are experiencing nutrient losses due to aversions. Lastly, pertaining to the antioxidant procurement hypothesis, it appears that, in the overwhelming majority of populations surveyed to date, fruits and fruit juices are among the most frequently reported pregnancy-related cravings (Flaxman & Sherman 2000; Olusanya & Ogundipe 2009; Weigel et al. 2011). Fruits and fruit juices not only represent sources of calories that are relatively low risk in terms of pathogenesis and chemical toxicity but also represent sources of a wide variety of necessary but hard-to-get antioxidants, especially vitamin A and zinc.

As the foregoing discussion implies, the hypotheses are not necessarily mutually exclusive. It is possible that all the challenges of pregnancy play a role in driving within- and among-population variations in expression of aversions and cravings during pregnancy. Some of the challenges may also underpin among-population variation in cultural phenomena such as food taboos relating to pregnancy, female-specific food taboos, and socially transmitted information about foods that may improve maternal and/or fetal health outcomes. Despite this possible compatibility among the hypotheses and despite proposed links between aversions and cravings, to our knowledge, no previous study has empirically treated food aversions and food cravings of pregnancy (and/or their cultural equivalents) as an adaptive complex that co-evolved to solve the suite of ecological and physiologic challenges imposed by gestation.

In our study, we aimed to integrate these multiple hypotheses pertaining to the physiologic challenges of pregnancy as we investigated patterning in food aversions and cravings of pregnancy as described by indigenous women from Yasawa Island, Fiji.

The remainder of the paper is organized into four sections. In the next section, section 2, we provide background information on the study site and on the lifeways and diets of the people of Yasawa Island, and discuss our methods. In section 3, we present the main results

of two sets of analyses in which we describe rates of foci for food aversions and cravings and we assess how cravings pattern in relation to aversions. In section 4, we partition the diets of Yasawa Islanders into three higher order categories – animal foods, starchy plant foods, and fruits and vegetables – and discuss the patterning of aversions and cravings within each of these higher order categories and offer suggestions as to how such patterning may relate to variation in expression of one or more of the physiologic challenges of pregnancy. In the final section, we engage in a broader discussion in which we summarize the available evidence regarding the evolutionary ecology of pregnancy-related food aversions and food cravings among the women of Yasawa Island, focusing particularly on possible interactions between the visceral changes in appetite reported in this paper and cultural regulation of pregnancy diet (reported in Henrich & Henrich 2010).

2. Population, data, and methods

The data for this study were collected as part of a larger, ongoing research project led by JH on social organization, ecology, life history, and culture on Yasawa Island, Fiji. Over several years, the team has gathered information from the men, women, and children of Yasawa about local subsistence economy, diet, food taboos, reproductive histories and demography, and cultural learning and transmission (Henrich & Henrich 2010; Henrich & Broesch 2011; Kline et al. 2013; Broesch et al. 2014; McKerracher et al. in press).

The 70 women interviewed regarding appetite sensations in pregnancy are from three villages located on Yasawa Island, on the northwest end of the Fijian archipelago. The climate on the island is warm year-round, but there are two seasons – a wet and a dry – marked sharply by variation in precipitation. The soils of the island are sandy and dry, but sufficient to produce a variety of root and fruit crops (see data supplement for Henrich & Henrich 2010).

The people of Yasawa are primarily small-scale fisher-farmers. Men in these communities fish and maintain garden plots while the women, with the assistance of older children, gather shellfish and other littoral resources and also carry out the majority of the domestic work. Additional details on the ethnographic context for this project are available in Henrich and Henrich (2010) and Henrich and Broesch (2011).

The diets of Yasawa Islanders are predominantly local. Cassava provides the majority of calories, although yams, plantains, breadfruit, and imported wheat and sugar also make important energetic contributions. Marine foods provide the bulk of the protein in the Yasawan diet. Fat derives from coconut milk and fish as well as from imported oil and small amounts of imported or local terrestrial meat. Local fruits and vegetables from the

gardens along with some imported dairy products likely offer a variety of micronutrients. Common beverages consumed include tea and "*yaqona*" (kava), a drink prepared from a root native to the Pacific that has mildly sedative properties. Information on how core dietary items were ranked relative to one another with respect to nutrient density is available in the supplementary online resources (Online resource 1, section 1).

All of the women in the sample had at least one child at the time of the interview (see Online Resource 1, section 2 for additional information on pregnancy and demography in the study population). To identify foci for pregnancy-related food aversions and cravings among the women of Yasawa Island, each participant was asked in Standard Fijian if there were any foods that she would normally eat and enjoy but that she found aversive during a past pregnancy. She was then asked if there were any foods she especially craved while pregnant. She was also asked if there were any foods she knew were taboo for pregnant women to eat, but we do not report the taboo responses here because those responses have already been presented elsewhere (Henrich & Henrich 2010). Following the freelist procedure, each woman was asked if any of 17 specific food types was aversive to her and/or craved by her during a previous pregnancy. These checklist responses were used to validate and to clarify the freelist responses. Further details on the checklist categories and on how the checklist information was used to refine the freelist information are available in the electronic supplementary resources (Online Resource 1, section 3).

We coded the responses into 10 categories, listed alphabetically in Table 2.

[Table 2]

After coding responses, we carried out two sets of analyses. First, we visually inspected bar graphs (produced in Microsoft Excel, Excel for Mac 2011, version 14.4.6) that represent the frequencies at which women spontaneously reported foods in a given category to be aversive and/or craved. Second, using χ^2 tests with Monte-Carlo 1000-replicate simulated p-values, we tested the prediction of the nutrient-seeking hypothesis that women likely to be experiencing nutrient losses due to aversions were more likely than other women to develop cravings for foods that could compensate for those losses. The latter analyses were carried out in the stat (R Development Core Team 2008).

3. Results

3.1. Overall results

The overall rates of aversions and cravings from the freelist responses are summarized in Online Resource 1, section 4, Table ESM4. We present the food category-based aversions and cravings data used in the first set of analyses in Figure 1 as well as in a table in the supplement (Online Resource 1, section 4, Table ESM5).

[Figure 1]

Regarding aversions, we found that 50 women (71% of the sample) reported developing at least one novel aversion during past pregnancies and twenty women (29% of the sample) reported having experienced no aversions. Three of these 50 women with aversions (4% of the sample) said they disliked all foods during the early phase of a past pregnancy.

The more detailed aversions data presented in Figure 1 focus on only the 47 women who experienced aversions to specific types of foods. For these women, fish was the most commonly aversive food, followed by cassava, meat, non-fish aquatic foods, imported starches, locally-grown starches and, rarely, spicy/sour/bitter tasting vegetables. Bananas/plantains and other fruits and vegetables were generally not considered aversive.

With respect to cravings, all 70 women in the sample reported experiencing at least one novel food craving during a past pregnancy. Fourteen of these women reported having either craved "all food," or, in two cases, any food prepared using a particular cooking method. For the remaining 56 women that identified more specific cravings for foods, bananas/plantains were the most frequently identified category of craved foods, followed by other fruits (especially mangos), other vegetables (especially leafy greens), fish, and meat. All other food categories were only rarely craved, with few women mentioning cravings for cassava, locally grown starches, imported starches, non-fish aquatic resources, or spicy/sour/bitter plant foods.

In general, more aversive foods were craved infrequently and more craved foods were aversive infrequently (Fig. 1). The obvious exception to this pattern is fish, which is by far the most aversive food category but is also craved at moderate frequencies.

With regard to the second set of analyses in which we used χ^2 tests to assess whether nutrient losses from aversions affect the foci for cravings, we found that women that developed aversions to specific foods within a food category were more likely than other women to develop specific cravings for alternate foods that meet similar nutritional needs. The risks for developing particular cravings in tandem with particular aversions are summarized in Table 3 and discussed in the three sections below.

[Table 3]

3.2 *Aversions to and cravings for fish, non-fish aquatic resources, and meat/dairy*

Fish represents the most important source of protein in Yasawan diets, followed distantly by other aquatic resources and by terrestrial meats (Online Resource 1, section 1 Table ESM1). Access to sufficient dietary protein is crucial to the development of an immunologically and metabolically robust human phenotype (e.g. Rice et al. 2000; Schaible & Stefan 2007), and maternal protein deficiencies during pregnancy predict infant and early childhood protein deficiencies (Forrester et al. 2012). So, *ceteris paribus*, we might expect reduced protein consumption during early pregnancy to have negative effects on infant health outcomes and thus on both maternal and offspring fitness.

We found, however, that fish was the food category most frequently identified as aversive by the women of Yasawa Island, with 41 women (87% of the sample with any specific food aversions) disliking the thought of eating fish during early pregnancy. Furthermore, 13 women (~28% of women with any specific aversions) developed novel aversions to terrestrial meat in addition to aversions to fish during pregnancy, despite the fact that terrestrial meat is only rarely encountered by Yasawan women. Another 13 women (11 of whom also had aversions to fish) reported novel aversions to non-fish aquatic foods.

One plausible explanation for the high rate at which women reported animal products (especially fish) as aversive derives from the maternal-embryo protection hypothesis. To reiterate, this hypothesis suggests that women have evolved cognitive mechanisms such as aversions to motivate them to avoid key sources of pathogens and chemical toxins when they are immune compromised by pregnancy. Several comparative studies have suggested that, because animal foods are subject to more rapid rates of spoilage and zoonotic parasitism/pathogenesis than plant foods and because pregnant women and their offspring are especially vulnerable to pathogenic insult, pregnant women in many populations generally find animal foods more aversive than plant foods (Flaxman & Sherman 2000; Fessler 2002a; Fessler et al. 2005). Animal foods are especially salient sources of pathogens on Yasawa and in other similar small-scale societies because there is no access to refrigeration, so such foods are typically stored at temperatures conducive to the rapid multiplication of disease-causing microbes for hours or sometimes days before being cooked and eaten.

Despite the finding that fish and other animal products were considered aversive during pregnancy by most Yasawan women, some foods from these food categories were identified by 20 women (36% of women with any specific cravings) as craved food items during pregnancy. This pattern may indicate that some women are poorly equipped to

afford the energetic and especially the protein, fatty acid, and micronutrient debits associated with excluding all or most animal foods from their diets. Consistent with this, women with aversions to fish (many of whom also had aversions to meat and/or non-fish aquatic foods) were nearly twice as likely to have specific cravings for high-protein foods such as specially prepared fish, meat/dairy, or shellfish than women without fish aversions. Thus, it may be that women who face the problem of protein or certain micronutrient shortages due to aversions to animal foods are motivated by cravings to focus on securing these nutrients from the few protein-dense foods that they do not find aversive.

3.3 *Aversions to and cravings for cassava and other starches*

Cassava provides the majority of calories for the people of Yasawa Island, followed by other kinds of starchy foods such as yams, breadfruit, bananas/plantains, and imported cereal products (Online Resource 1, section 1, ESM1). Yet, 26 women (55% of those who reported any specific food aversions) identified cassava as being aversive during early pregnancy. Aversions to other kinds of starchy foods (even pooling all non-cassava starches) were far less common than those to cassava. Nonetheless, 17 women (36% with any specific aversions) reported one or more aversions to imported or locally grown starches. Eleven of these 17 women with aversions to imported or locally grown starches also had aversions to cassava. These aversions to staple, starchy foods that provide the bulk of the calories to Yasawan Islanders are surprising, given that pregnancy increases a woman's daily energetic requirements and that such foods are among the least aversive and the most craved in well-studied, Western populations (Flaxman & Sherman 2000).

The maternal embryo protection hypothesis supplies a potential explanation for the high rates of pregnancy-related aversion to cassava in this population. Cassava contains cyanide-producing compounds at levels that can impede development and increase morbidity and mortality in fetuses exposed in utero (e.g. Lancaster et al. 1982; Nhassico et al. 2008; see also Frakes et al. 1986 on effects of cyanide in pregnancy on rodent models). Cyanide levels may be especially high in cassava cultivated in dry, sandy soils such as those of Yasawa (see, for example, Cadavid et al. 1998; El-Sharkawy 2006). Anecdotally, several women in the Yasawa sample reported that the smell, the taste, or both the smell and taste of cassava were unappealing during pregnancy. So, it may be that the pregnant women of Yasawa are detecting olfactory and/or gustatory cues to the teratogenicity of cassava, finding those cues aversive, and thus reducing the risk of fetal exposure to the chemical toxin cyanide.

Because protein deficiency increases susceptibility to chemical poisoning from cyanide (Frakes et al. 1986; Teles 2002), if women are averse to cassava because of its chemical

toxicity, we should expect pregnant women with low protein diets to be especially averse to cassava. The evidence from the women of Yasawa is consistent with this prediction Women with fish, meat, and shellfish aversions are more likely to face protein deficiencies and thus are at elevated risk of cyanide poisoning from cassava consumption. We found that 24 of the 44 women with aversions to animal foods (56%) also reported aversions to cassava whereas only two of the 26 women without aversions to animal foods (8%) reported aversions to cassava.

Regarding forms of starch other than cassava, the gestational metabolic syndrome avoidance hypothesis and the compensatory placental growth hypothesis both predict that pregnant women may develop aversions to such foods. However, the compensatory placental growth hypothesis predicts that all kinds of energy-dense foods should also be aversive, and we find little evidence to support this (see Online Resource 1, sections 1 and 4, Tables ESM1 and ESM5; see also McKerracher et al. in press). So, we think the gestational metabolic syndrome avoidance hypothesis offers a more plausible explanation for aversions to non-toxic starches than the compensatory placental growth hypothesis, at least in this population. As we explained earlier, the logic of the gestational metabolic syndrome avoidance hypothesis is that maternal metabolism impairs absorption of sugars (Butte 2000) and alters blood pressure regulation (Redman et al. 1999) in healthy pregnancies, such that relatively more energy is circulating and available to cross the placenta for use in fetal growth and development (Haig 1993). While both increased tolerance of circulating sugars and increased blood pressure in pregnant women relative to non-pregnant women can positively impact fetal health outcomes, more extreme versions of these phenomena (gestational diabetes and preeclampsia, respectively) pose significant risks to both maternal and fetal health and survivorship (Young et al. 2010; Ryckman et al. 2013). As Brown et al. (2013) suggest, women may have evolved adaptations to reduce the risk of expressing these more extreme, pathological phenotypes, especially in ecological conditions in which the sugar needed for normal fetal growth is readily and consistently available from the diet.

One strategy to reduce the risks of developing gestational diabetes and preeclampsia involves developing aversions to foods implicated in the etiology of gestational metabolic syndromes. This strategy is energetically costly because it encourages pregnant women to avoid key sources of energy. So, among women that are at low genetic risk for developing gestational metabolic syndromes (specifically, women of European descent), this strategy is uncommon and aversions to starches and sugars are rare (see reviewed literature in Flaxman & Sherman 2000 p. 126-127). However, the aversions strategy may represent a more flexible solution to the problems posed by gestational metabolic syndromes for women from populations with diets in which, historically, the sugar needed for fetal growth was not consistently available, either due to unavailability of cereal grains and starches or

due to intense and regular famine cycles. The women from Yasawa Island are from a population without a long history of reliance on cereal products and sugars or secure availability of other starches, so some of the women from this population may develop food aversions to starchy foods during pregnancy to reduce their consumption of foods that promote the expression of gestational metabolic syndromes. Consistent with this reasoning, foods most likely to promote the development of gestational diabetes such as white flour products, white rice, and breadfruit (see Atkinson et al. 2008) were reported as being aversive more frequently than other plant foods such as bananas, coconuts, mangos, and papayas by Yasawa women. Similar or more extreme patterns of developing pregnancy-related aversions to some kinds of starchy foods have recently been observed in other populations without long histories of consuming refined sugars and starches, such as the Datoga, the Turkana (Young & Pike 2012), and the Pemba Island peoples of East Africa (Steinmetz et al. 2012) and the predominantly Mestizo people of urban Ecuador (Weigel et al. 2011). Thus, the women of Yasawa Island along with women from other populations that have not traditionally consumed large quantities of cereal and sugar products appear to express aversions to such foods, and these aversions may represent a solution to the problems of morbidity and mortality from gestational metabolic syndromes.

While pregnancy-related aversions to cassava may protect mothers and fetuses from the harmful effects of cyanide poisoning and aversions to starches in general may offer protection from gestational metabolic syndromes, these aversions nonetheless likely have high energetic and health costs. Substantial calorie restrictions during pregnancy impact both short- and long-term offspring outcomes, and are associated with reduced neonatal and early childhood survivorship as well as increased risks of developing non-communicable metabolic diseases in both childhood and adulthood (Hales & Barker 1992; Gluckman & Hanson 2004; Dulloo et al. 2006; Wells 2009; Godfrey et al. 2010; 2011; Patti 2013; Wood-Bradley et al. 2013). As such, cassava and other starch avoidances during pregnancy reduce the risk of developing feto-toxicity and gestational metabolic syndromes, but simultaneously impair gestational nutrition. Many Yasawan women may attempt to solve this problem of nutrient losses from starch aversions by developing cravings for bananas and plantains or, occasionally, for other types of energy-dense foods. In line with this expectation, we found that, of the 26 women with aversions specifically to cassava, 18 women (60%) specifically reported cravings for bananas/plantains and/or other starchy foods. These banana/plantain and starch cravings were much more common in the subsample of women with cassava aversions than the subsample without (see Table 3). The other eight women with cassava aversions craved other energy dense foods, citing specific desires for fish, meat, or milk; such cravings were at least slightly more prevalent in the cassava averse group than in the group without cassava aversions. Additionally, cravings for foods with low energy densities but high micronutrient yields (e.g. mango, pawpaw,

hibiscus leaves, and spinach) were relatively rare for the women with cassava aversions but common for women with other specific aversions (although this difference is not statistically significant), tentatively suggesting that the women with aversions to staple starches focus on meeting energy requirements before meeting other nutritional needs. These findings are consistent with the hypothesis that women with starch aversions experience cravings that motivate them to seek foods that can compensate for some of the caloric losses associated with not consuming staple crops.

3.4 *Aversions to and cravings for fruits and vegetables*

Few women from Yasawa Island reported aversions to fruits or to mild-tasting vegetables but many women reported cravings for foods from these food categories. With respect to spicy/sour/bitter plant foods, five women (~11% of women with any specific aversions) identified chili, curry, lime, and/or tea as aversive.

The low frequency of aversions to fruits or vegetables among Yasawan women is consistent with the maternal-embryo protection hypothesis, the compensatory placental growth hypothesis, and the gestational metabolic syndrome avoidance hypothesis. Aside from some starchy or spicy/sour/bitter vegetables, plant foods constitute low risk foods with respect to pathogenesis, teratogenesis, fetal-biased nutrient partitioning, or gestational metabolic syndromes. So, since these foods pose few morbidity or mortality risks to pregnant women or to fetuses relative to animal products, adaptive hypotheses for pregnancy-related food aversions predict that women should rarely develop aversions to fruits and vegetables.

The finding that some of the women of Yasawa Island developed aversions to chili, curry, lime, and tea is also consistent with the adaptive hypotheses for pregnancy-related food aversions. Aversions to strong tasting plant foods are expected under the maternal-embryo protection hypothesis, because such flavours typically indicate the presence of chemicals produced by the plant as a toxic deterrent against consumption by other organisms (Profet 1988; 1992; 1997; Billing & Sherman 1998; Sherman & Hash 2001; Fessler & Navarrete 2003). While the extent to which the consumption of such foods actually affect human embryo development is unclear (e.g. Brown et al. 1997; Christian & Brent 2001; Chanda et al. 2006), it may be that some women are responding to olfactory or gustatory cues about the possible chemical toxicity of these plant foods and are thus developing aversions to them (Flaxman & Sherman 2000; Sherman & Flaxman 2002).

While fruits and mild-tasting vegetables were rarely identified as aversive by the Yasawan women, these two categories together constitute foci for pregnancy-related food cravings among 30 women (54% of women with any specific cravings). This finding is similar to

what has been documented for many other populations: fruits and mild-tasting vegetables are consistently among the most frequently craved food items in pregnancy in populations from Europe and North America (Flaxman & Sherman 2000), South America (Weigel et al. 2011), and Sub-Saharan Africa (Steinmetz et al. 2012).

The existing evolutionary literature on appetite sensations offers the nutrient-seeking hypothesis as an explanation for the high prevalence of cravings for fruit and mild-tasting vegetables during pregnancy. This hypothesis holds that such foods provide a low risk source of nutrients for women during pregnancy, a life stage in which consumption of many other foodstuffs is especially risky to both mother and offspring (Fessler 2002). Thus, women may develop cravings for fruits and vegetables because such cravings motivate them to seek out at least some calories and other nutrients when aversions to meats and starches otherwise limit dietary intake and when fetal growth demands resources from mothers. As outlined earlier in the text, we propose an additional hypothesis, complementary to the first. This additional hypothesis, the antioxidant procurement hypothesis, suggests that women may crave fruits and vegetables because such foods represent dietary sources of antioxidants, which may reduce oxidative stress of pregnancy and its associated risks of pregnancy complications or loss.

The pregnancy-related food cravings data from Yasawan women support both hypotheses and point to the need for further investigation of this second, alleviation of oxidative stress hypothesis. As mentioned above, antioxidant rich foods were among the most frequently craved foods during pregnancy in this population. We also found that women expected to be under relatively low levels of oxidative stress because they have diets relatively low in oxidant-producing molecules craved antioxidant rich foods at lower frequencies than women expected to be under higher levels of oxidative stress. That is, we assumed that pregnant women that craved meat and grilled food (foods containing high loads of reactive oxygen species) are unlikely to have consumed excesses of these oxidant-producing foods and are thus less likely to be under extreme oxidative stress than other women with diets richer in meat and cooked foods. Only ~11% of these women with cravings for oxidant-producing foods craved foods rich in antioxidants whereas 48% of women without cravings for oxidant-producing foods craved foods rich in antioxidants (see Table 3).

4. Implications of pregnancy-related food aversions and cravings for human evolution and avenues for future research

The evidence reported here suggests that pregnancy-related food aversions and cravings in the women of Yasawa Island are strongly patterned. These patterns are generally consistent with the expectations of several adaptive hypotheses proposed to explain why food aversions and cravings co-occur with one another and with five physiological challenges posed by pregnancy. That is, most of the women of Yasawa Island reported pregnancy-related aversions to particular foods that they would normally enjoy and all of the women in this population reported experiencing pregnancy-related food cravings. The foods found to be aversive most frequently were fish and cassava, followed by other animal foods and other starches. Yasawan women most often craved bananas/plantains followed by other kinds of less starchy fruit and by mild-tasting vegetables. Women that experienced specific aversions were more likely than other women to report cravings for foods that would replace nutrient losses due to those aversions. The finding that women frequently reported aversions to fish, other animal foods, and cassava – foods likely to contain pathogens or chemical toxins disruptive to maternal health and to fetal development – is consistent with the maternal-embryo protection hypothesis. The observation that women from this population develop aversions to foods implicated in the etiology of gestational diabetes such as refined starches is in keeping with the predictions of the gestational metabolic syndrome avoidance hypothesis or possibly the compensatory placental growth hypothesis. The results regarding cravings foci accord with the predictions of the nutrient-seeking hypothesis and with the predictions of the antioxidant procurement hypothesis.

Taken together, this series of findings regarding focal categories for food aversions and cravings among Yasawan women may have a number of implications for understanding human ecology and evolution and suggest avenues for future research. With respect to implications for human ecology and evolution, our findings are consistent with the view that pregnancy-related food aversions and cravings evolved to motivate women to reduce risks and stresses to themselves and to their offspring during pregnancy, perhaps evoked via the smell and/or taste of particular local dietary categories. Pregnancy presents a major opportunity for selection on maternal and offspring behaviour, physiology, immunology, and metabolism (Brown et al. 2013). Fetal, infant, and maternal mortality directly account for nearly one third of all mortality both in historically documented pre-modern and in contemporary under-developed societies (Graunt 1662, cited in Brown et al. 2013; Lozano et al. 2013), and this figure would be substantially higher if embryonic mortality were also taken into account (e.g. Nepomnaschy et al. 2006). With these mortality rates in mind, we should expect contemporary mothers, as descendants of mothers that successfully avoided the high mortality risks associated with pregnancy, to have strategies to reduce mortality risks during their own pregnancies (Fessler 2002; Steinmetz et al. 2012). In particular, mothers are expected to possess mechanisms that discourage them from eating foods that exacerbate pathogenesis, exposure to fetal developmental insult, and metabolic and

oxidative stresses. Aversions to animal foods, chemically toxic plant foods, and highly glycemic plant foods among the women of Yasawa Island as well as in other, previously studied populations may represent such evolved strategies. We should also expect mothers to possess mechanisms that encourage them to eat foods that can provide the nutrients necessary for healthy fetal development as well as for their own somatic maintenance. Cravings for foods with relatively low pathogen and teratogen loads, relatively low glycemic loads, and relatively rich contributions of calories, protein, fatty acids, and antioxidants likely reflect motivational mechanisms that drive mothers to prioritize seeking out foods that reduce stress and promote tissue maintenance and generation.

In this paper, we focused on visceral aversions and cravings and did not investigate the roles of culture and cultural evolution in pregnancy diet. However, a previous study by Henrich and Henrich (2010) shows that Yasawa Islanders have developed cultural prohibitions, enforced through scolding and reputation management, that prevent pregnant and lactating women from ingesting marine foods that are likely to carry the biochemical toxin ciguatera, a known teratogen (Pearn et al. 1982). The women participating in this study clearly distinguished between foods that were "taboo" and foods that they simply disliked the sight, smell, taste, and/or thought of. Many aversive foods are not tabooed and many tabooed foods are not aversive. The taboos apply to a much smaller number of food items (some of which are only rarely encountered and eaten), and women generally agree about which foods are taboo. These prohibitions appear effective, because pregnant and breastfeeding women experience ciguatera poisoning at much lower rates than other members of the population (Henrich & Henrich 2010). Thus, the evidence suggests that Yasawa Islanders use culturally transmitted information to solve a complicated, locally specific ecological problem pertaining to pregnancy physiology and diet. By contrast with tabooed foods for which there is high consensus about what foods should be avoided, the aversions discussed here, while also often focused on marine foods that might contain ciguatera, encompass a relatively diverse array of foods and vary substantially among individuals. We propose that whether women express aversions at all and to which specific foods they develop aversions are factors likely contingent on inter-individual variation in nutritional status, especially variation in protein, fatty acid, and micronutrient sufficiency. If our proposal is correct, aversions may reflect a genetically based predisposition of women to develop aversions to any foods that are salient with respect to diseases and/or toxicity, but that are only evoked by relevant foods from the local diet when women can afford the nutrient costs of such aversions. This hypothesis aligns with one of Holland and O'Brian (2003), which poses that genetic mechanisms for appetite suppression in pregnancy are most likely to have evolved under the condition that women were not constantly facing severe nutritional shortfall. Culturally transmitted taboos, in contrast, inhibit all pregnant women, regardless of inter-individual variation in health parameters,

from eating especially dangerous foods. Thus, it appears that aversions and taboos may have evolved in parallel via different transmission mechanisms to solve related but nonetheless distinct classes of ecological challenges faced during pregnancy.

With respect to future research, our first objective will be to address the main shortcomings of the present study. Specifically, while we found that the data on food aversions and cravings among Yasawan women are *consistent* with the reasoning that food aversions reduce maternal and fetal exposure to a variety of insults and that cravings motivate mothers to acquire nutrients necessary both for their own and for fetal health, we do not yet have adequate data to directly test all five of the adaptive hypotheses. In particular, we lack pregnancy-by-pregnancy information on maternal nutritional status, adiposity, and diet, and such data are necessary to formally test the gestational metabolic syndrome avoidance hypothesis, the nutrient-seeking hypothesis, and the antioxidant procurement hypothesis. Furthermore, we do not yet have pregnancy-by-pregnancy data on fetal/infant outcomes, so we cannot assess the fitness consequences of pregnancy food avoidances and consumption in this population. In a companion paper that focused exclusively on aversions of pregnancy (McKerracher et al. in press), we used data from the women of Yasawa Island to formally test predictions of the two hypotheses for which we do have some appropriate data, the maternal-embryo protection hypothesis and the compensatory placental growth hypothesis. In that study, we found that food aversions of pregnancy in this population focus preferentially on foods of relatively high pathogen risk and chemical toxicity rather than foods with relatively high energy density, lending some support to the maternal-embryo protection hypothesis and casting some doubt on the utility of the compensatory placental growth hypothesis. These findings indicate that we can reject the null hypothesis of no impact of food category composition on food category aversiveness, and suggest that further evaluation of adaptive hypotheses for pregnancy-related changes in diet is warranted. With the foregoing in mind, future studies on Yasawa Island and in other populations should directly and prospectively test whether women preferentially experience cravings for starches or other energy-dense foods when they are calorie-stressed, meat or other protein-dense foods when they are protein and/or micronutrient stressed, and fruits and vegetables when they are experiencing especially high loads of oxidative stress. They should also test whether food aversions, food cravings, and interactions between food aversions and cravings impact fetal survivorship and indicators of subsequent maternal and infant health.

We also aim to further investigate the relationship between food aversions and taboos in pregnancy in future work, paying particular attention to inter-individual variations likely to promote or repress expression of aversions. In a similar vein, we intend to explore the role of cultural evolution in the development and acquisition of food cravings. Recently, Young and Pike (2012) reported findings on food cravings among the Turkana and Datoga

pastoralists of East Africa. They found that, at least anecdotally, women reported experiencing concerns over supplying their babies with adequate nutrition. They also reported that local wise women offered advice on the foods that pregnant women should eat so as to promote the health and growth of their future children. Among the women of Yasawa Island, at least one participant spontaneously reported that she was averse to all foods but that she made herself eat various things "for the sake of the baby." Similar phenomena are well-documented in Western contexts, with health practitioners, public policy-makers, researchers, and members of mothers' social circles regularly offering advice on what nutrients women should seek out from specific foods to optimize fetal health and with pregnant women being especially attuned to the need to eat healthfully (Anderson et al. 1993; Gardner et al. 2012). These examples constitute tantalizing clues that suggest that, across varying social and ecological contexts, cultural systems have developed and are continuing to develop information regarding diet in pregnancy that is socially transmittable, so as to optimize maternal and fetal health for cultural group members. Systematic, quantitative research is needed – in both Yasawa Islanders and in other populations – concerning the factors that influence the development of these socially-learned diet recommendations and concerning how such cultural factors interact with physiological craving sensations.

In conclusion, taking the findings of the present study together with the findings of our study on aversions and nausea and vomiting of pregnancy (McKerracher et al. in press) and on the findings of Henrich and Henrich (2010), the current evidence suggests that the women of Yasawa have access to at least two main strategies for overcoming the substantial adaptive challenges posed by pregnancy, one genetically transmitted but evoked by local ecological circumstances, the other socially transmitted. These findings highlight the usefulness of studying human physiological and behavioural phenomena within an integrated evolutionary ecological framework that accounts for both genetic and cultural inheritance.

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References

Al-Gubory, K. H. (2013) Maternal nutrition, oxidative stress and prenatal developmental outcomes. In: Studies on Women's Health (Ed. by A. Agarwal, N. Aziz & B. Rizk), pp. 1-31. Springer.

Anderson, A., Campbell, D. & Shepherd, R. (1993) Nutrition knowledge, attitude to healthier eating and dietary intake in pregnant compared to non- pregnant women. Journal of Human Nutrition and Dietetics, **6**, 335-353.

Atkinson, F. S., Foster-Powell, K. & Brand-Miller, J. C. (2008) International tables of glycemic index and glycemic load values: 2008. Diabetes Care, **31**, 2281-2283.

Billing, J. & Sherman, P. W. (1998) Antimicrobial functions of spices: why some like it hot. Quarterly Review of Biology, **73**, 3-49.

Broesch, J., Barrett, H. C. & Henrich, J. (2014) Adaptive Content Biases in Learning about Animals across the Life Course. Human Nature, **25**, 181-199.

Brown, E. A., Ruvolo, M. & Sabeti, P. C. (2013) Many ways to die, one way to arrive: how selection acts through pregnancy. Trends in Genetics, **29**, 585-592.

Brown, J. E., Kahn, E. S. & Hartman, T. J. (1997) Profet, profits, and proof: Do nausea and vomiting of early pregnancy protect women from "harmful" vegetables? American Journal of Obstetrics and Gynecology, **176**, 179-181.

Butte, N. F. (2000) Carbohydrate and lipid metabolism in pregnancy: normal compared with gestational diabetes mellitus. The American Journal of Clinical Nutrition, **71**, 1256s-1261s.

Cadavid, L., El-Sharkawy, M. A., Acosta, A. & Sánchez, T. (1998) Long-term effects of mulch, fertilization and tillage on cassava grown in sandy soils in northern Colombia. Field Crops Research, **57**, 45-56.

Chanda, S., Sharper, V., Hoberman, A. & Bley, K. (2006) Developmental toxicity study of pure trans-capsaicin in rats and rabbits. International journal of toxicology, **25**, 205-217.

Christian, M. S. & Brent, R. L. (2001) Teratogen update: evaluation of the reproductive and developmental risks of caffeine. Teratology, **64**, 51-78.

Crespi, B. & Badcock, C. (2008) Psychosis and autism as diametrical disorders of the social brain. Behavioral and Brain Sciences, **31**, 241-260.

Crespi, B. J. (2011) The strategies of genes: Genomic conflicts, attachment theory, and the development of the social brain. In: *Brain, Behavior, and Epigenetics* (Ed. by A. Petronis & J. Mill), pp. 143. Berlin, Heidelberg:Springer.

Crespi, B. J. (2010) The origins and evolution of genetic disease risk in modern humans. Annals of the New York Academy of Sciences, **1206**, 80-109.

Das, R., Hampton, D. D. & Jirtle, R. L. (2009) Imprinting evolution and human health. Mammalian Genome, **20**, 563-572.

Drewnowski, A. (1997) Taste preferences and food intake. Annual Review of Nutrition, **17**, 237-253.

Dufour, D. L. & Sauther, M. L. (2002) Comparative and Evolutionary Dimensions of the Energetics of Human Pregnancy and Lactation. American Journal of Human Biology, **14**, 585-602

Dulloo, A. G., Jacquet, J., Seydoux, J. & Montani, J. (20060 The thrifty 'catch-up fat' phenotype: its impact on insulin sensitivity during growth trajectories to obesity and metabolic syndrome. International Journal of Obesity, **30**, S23-S35.

Eaton, B. & Konner, M. (1985) Palaeolithic nutrition. A consideration of its nature and current implications. New England Journal of Medicine, **312**, 283-289.

El-Sharkawy, M. (2006) International research on cassava photosynthesis, productivity, eco-physiology, and responses to environmental stresses in the tropics. Photosynthetica, **44**, 481-512.

Fessler, D. M. T. (2002a) Reproductive Immunosuppression and Diet: An Evolutionary Perspective on Pregnancy Sickness and Meat Consumption. Current Anthropology, **43**, 19.

Fessler, D. M. T. & Navarrete, C. D. (2003) Meat Is Good to Taboo: Dietary proscriptions as a product of the interation of psychological mechanisms and social processes. Journal of Cognition and Culture, **3**, 1-40.

Fessler, D. M. T., Eng, S. J. & Navarrete, C. D. (2005) Elevated disgust sensitivity in the first trimester of pregnancy. Evolution and Human Behavior, **26**, 344-351.

Flaxman, S. M. & Sherman, P. W. (2008) Morning Sickness : Adaptive Cause or Nonadaptive Consequence of Embryo Viability? The American Naturalist, **172**, 54-62.

Flaxman, S. M. & Sherman, P. W. (2000) Morning Sickness: A Mechanism for Protecting Mother and Embryo. The Quarterly Review of Biology, **75**, 113-148.

Forrester, T. E., Badaloo, A. V., Boyne, M. S., Osmond, C., Thompson, D., Green, C., Taylor-Bryan, C., Barnett, A., Soares-Wynter, S. & Hanson, M. A. (2012) Prenatal factors contribute to the emergence of kwashiorkor or marasmus in severe undernutrition: evidence for the predictive adaptation model. PloS ONE, **7**, e35907.

Frakes, R. A., Sharma, R. P., Willhite, C. C. & Gomez, G. (1986) Effect of cyanogenic glycosides and protein content in cassava diets on hamster prenatal development. Fundamental and applied toxicology, **7**, 191-198.

Gardner, B., Croker, H., Barr, S., Briley, A., Poston, L. & Wardle, J. (2012) Psychological predictors of dietary intentions in pregnancy. Journal of Human Nutrition and Dietetics, **25**, 345-353.

Gerber, L. M., Williams, G. C. & Gray, S. J. (1999) The nutrient-toxin dosage continuum in human evolution and modern health. Quarterly Review of Biology, **74**, 273-289.

Gluckman, P. D. & Hanson, M. A. (2004) Living with the past: evolution, development, and patterns of disease. Science, **305**, 1733-1736.

Godfrey, K. M., Gluckman, P. D. & Hanson, M. A. (2010) Developmental origins of metabolic disease: life course and intergenerational perspectives. Trends in Endocrinology & Metabolism, **21**, 199-205.

Haig, D. (1993) Genetic conflicts in human pregnancy. Quarterly Review of Biology, **68**, 495-532.

Haig, D. (1999) Genetic conflicts of pregnancy and childhood. Evolution in health and disease, In: Evolution in Health and Disease (Ed. by Stearns, SC and Koella, JC). Oxford: Oxford University Press, pp. 77-90.

Hales, C. N. & Barker, D. J. (1992) Type 2 (non-insulin-dependent) diabetes mellitus: the thrifty phenotype hypothesis. Diabetologia, **35**, 595-601.

Henrich, J. & Broesch, J. (2011) On the nature of cultural transmission networks: evidence from Fijian villages for adaptive learning biases. Philosophical Transactions of the Royal Society B: Biological Sciences, **366**, 1139-1148.

Henrich, J. & Henrich, N. (2010) The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins. Proceedings of the Royal Society B: Biological Sciences, **277**, 3715.

Holland, T. D. & O'Brien, M. J. (2003) On Morning Sickness and the Neolithic Revolution1. Current anthropology, **44**, 707-711.

Hook, E. B. (1978) Dietary cravings and aversions during pregnancy. The American Journal of Clinical Nutrition, **31**, 1355-1362.

Hook, E. B. (1980) Influence of pregnancy on dietary selection. International Journal of Obesity, **4**, 338-340.

Huxley, R. R. (2000) Nausea and vomiting in early pregnancy: Its role in placental development. Obstetrics & Gynecology, **95**, 779-782.

Jauniaux, E., Poston, L. & Burton, G. J. (2006) Placental-related diseases of pregnancy: involvement of oxidative stress and implications in human evolution. Human Reproduction Update, **12**, 747-755.

Kline, M. A., Boyd, R. & Henrich, J. (2013) Teaching and the life history of cultural transmission in Fijian villages. Human Nature, **24**, 351-374.

Lancaster, P., Ingram, J., Lim, M. & Coursey, D. (1982) Traditional cassava-based foods: survey of processing techniques. Economic Botany, **36**, 12-45.

Langley-Evans, S. C. (2006) Developmental programming of health and disease. Proceedings of the Nutrition Society, **65**, 97-105.

Lozano, R., Naghavi, M., Foreman, K., Lim, S., Shibuya, K., Aboyans, V., Abraham, J., Adair, T., Aggarwal, R. & Ahn, S. Y. (2013) Global and regional mortality from 235 causes of death for 20 age groups in 1990 and 2010: A systematic analysis for the Global Burden of Disease Study 2010. The Lancet, **380**, 2095-2128.

Lunney, L. H. (1998) Compensatory placental growth after restricted maternal nutrition in early pregnancy. Placenta, **19**, 105.

McKerracher, L., Collard, M. & Henrich, J. (in press). The expression and adaptive significance of pregnancy-related nausea, vomiting, and aversions on Yasawa Island, Fiji. Evolution and Human Behavior. doi: http://dx.doi.org/10.1016/j.evolhumbehav.2014.09.005.

Myatt, L. (2006) Placental adaptive responses and fetal programming. The Journal of Physiology, **572**, 25-30.

Nepomnaschy, P. a., Welch, K. B., McConnell, D. S., Low, B. S., Strassmann, B. I. & England, B. G. (2006) Cortisol levels and very early pregnancy loss in humans. Proceedings of the National Academy of Sciences of the United States of America, **103**, 3938-42.

Nhassico, D., Muquingue, H., Cliff, J., Cumbana, A. & Bradbury, J. H. (2008) Rising African cassava production, diseases due to high cyanide intake and control measures. Journal of the science of food and agriculture, **88**, 2043-2049.

Olusanya, J. O. & Ogundipe, F. O. (2009) Food aversion and craving among pregnant women in Akure, Ondo State, Nigeria. International Journal of Tropical Medicine, **4**, 100-103.

Paine, M. A., Ruder, E. H., Hartman, T. J., Blumberg, J. & Goldman, M. B. (2013) Oxidative stress, oogenesis and folliculogenesis. In: Studies on Women's Health (Ed. by Anonymous), pp. 75-94. Springer.
Patil, C. L. & Young, S. L. (2012) Biocultural Considerations of Food Cravings and Aversions: An Introduction. Ecology of Food and Nutrition, **51**, 365-373.
Patti, M. 2013. Intergenerational programming of metabolic disease: evidence from human populations and experimental animal models. Cellular and Molecular Life Sciences,, 1-12.
Pearn, J., Harvey, P., De Ambrosis, W., Lewis, R. & McKay, R. (1982) Ciguatera and pregnancy. Medical Journal of Australia, **1**, 57-58.
Pepper, G. V. & Roberts, S. C. (2006) Rates of nausea and vomiting in pregnancy and dietary characteristics across populations. Proceedings of the Royal Society B: Biological Sciences, **273**, 2675-9.
Profet, M. (1997) Pregnancy Sickness: Using Your Body's Natural Defenses to Protect Your Baby-to-Be. Reading: Perseus.
Profet, M. (1992) Pregnancy sickness as adaptation: A deterrent to maternal ingestion of teratogens. In: The Adapted Mind (Ed. by J. H. Barkow, L. E. Cosmides & J. E. Tooby), pp. 327. New York: Oxford University Press.
Profet, M. (1988) The evolution of pregnancy sickness as protection to the embryo against Pleistocene teratogens. Evolutionary Theory, **8**, 177-190.
R Development Core Team. (2008) R: A language and environment for statistical computing.
Redman, C. W., Sacks, G. P. & Sargent, I. L. (1999) Preeclampsia: an excessive maternal inflammatory response to pregnancy. American Journal of Obstetrics and Gynecology, **180**, 499-506.
Rice, A. L., Sacco, L., Hyder, A. & Black, R. E. (2000) Malnutrition as an underlying cause of childhood deaths associated with infectious diseases in developing countries. Bulletin of the World Health Organization, **78**, 1207-1221.
Rillamas-Sun, E. (2010) The developmental origins of health and disease in women from the Michigan Bone Health Study: An examination with longitudinal and intergenerational data. PhD Dissertation. University of Michigan.
Rozin, P. & Vollmecke, T. A. (1986) Food likes and dislikes. Annual Review of Nutrition, **6**, 433-456.
Ryckman, K. K., Borowski, K. S., Parikh, N. I. & Saftlas, A. F. (2013) Pregnancy Complications and the Risk of Metabolic Syndrome for the Offspring. Current Cardiovascular Risk Reports, **7**, 217-223.
Savitz, D., Janevic, T., Engel, S., Kaufman, J. & Herring, A. (2008) Ethnicity and gestational diabetes in New York City, 1995–2003. BJOG: An International Journal of Obstetrics & Gynaecology, **115**, 969-978.
Schaible, U. E. & Stefan, H. (2007) Malnutrition and infection: complex mechanisms and global impacts. PLoS Medicine, **4**, e115.
Sclafani, A. 1997. Learned controls of ingestive behaviour. Appetite, **29**, 153-158.
Sherman, P. W. & Flaxman, S. M. (2001) Protecting ourselves from food. American Scientist, **89**, 142-151.

824 **Sherman, P. W. & Hash, G. A. (**2001) Why vegetable recipes are not very spicy. Evolution and
825 Human Behavior, **22**, 147-163.
826 **Sherman, P. W. & Flaxman, S. M. (**2002) Nausea and Vomiting of Pregnancy in an
827 Evolutionary Perspective. American Journal of Obstetrics & Gynecology, **186**, 190-197.
828 **Steinmetz, A. R., Abrams, E. T. & Young, S. L. (**2012) Patterns of nausea, vomiting, aversions,
829 and cravings during pregnancy on Pemba Island, Zanzibar, Tanzania. Ecology of Food and
830 Nutrition, **51**, 418-430.
831 **Svensson-Arvelund, J., Ernerudh, J., Buse, E., Cline, J. M., Haeger, J., Dixon, D., Markert,**
832 **U. R., Pfarrer, C., De Vos, P. & Faas, M. M. (**2013) The placenta in toxicology, part II:
833 Systemic and local immune adaptations in pregnancy. Toxicologic Pathology, **42**, 327.
834 **Teles, F. F. F. (**2002) Chronic poisoning by hydrogen cyanide in cassava and its prevention in
835 Africa and Latin America. Food & Nutrition Bulletin, **23**, 407-412.
836 **Tierson, F. D., Olsen, C. L. & Hook, E. B. (**1985) Influence of cravings and aversions on diet in
837 pregnancy. Ecology of Food and Nutrition, **17**, 117-129.
838 **Trivers, R. L. (**1974) Parent-offspring conflict. American Zoologist, **14**, 249-264.
839 **Weigel, M. M., Coe, K., Castro, N. P., Caiza, E., Tello, N. & Reyes, M. (**2011) Food Aversions
840 and Cravings during Early Pregnancy: Association with Nausea and Vomiting. Ecology of Food
841 and Nutrition, **50**, 197-214.
842 **Wells, J. (**2009) Thrift: a guide to thrifty genes, thrifty phenotypes and thrifty norms.
843 International journal of obesity, **33**, 1331-1338.
844 **Wells, J. C. (**2011) The thrifty phenotype: An adaptation in growth or metabolism? American
845 Journal of Human Biology, **23**, 65-75.
846 **Williams, G. C. & Nesse, R. M. (**1991) The dawn of Darwinian medicine. Quarterly Review of
847 Biology, **66**, 1-22.
848 **Wood-Bradley, R. J., Henry, S. L., Vrselja, A., Newman, V. & Armitage, J. A. (**2013)
849 Maternal dietary intake during pregnancy has longstanding consequences for the health of her
850 offspring. Canadian journal of physiology and pharmacology, **91**, 412-420.
851 **Young, A. G. & Pike, I. L. (**2012) A biocultural framework for examining maternal cravings and
852 aversions among pastoral women in East Africa. Ecology of Food and Nutrition, **51**, 444-462.
853 **Young, B. C., Levine, R. J. & Karumanchi, S. A. (**2010) Pathogenesis of preeclampsia. Annual
854 Review of Pathological Mechanical Disease, **5**, 173-192.
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856 **Table 1: Hypotheses and predictions regarding food aversions and cravings**

Hypothesis	Challenge of pregnancy	Tenets	Predicted aversive or craved food categories	References
Fetal protection	Embryo tissue different-iation (2)	Mothers selected to avoid chemical toxins in food to prevent fetal teratogenesis	Foods high in anti-microbial chemical compounds such as spicy, sour, bitter plant foods	Hook, 1978; Profet 1992
Maternal-embryo protection	Adaptive immune suppression, Embryo tissue different-iation (1,2)	Mothers selected to avoid disease-causing microbes and chemical toxins in food to prevent maternal illness and fetal developmental insult	Foods with high spoilages rates such as fish and meat, foods high in anti-microbial chemical compounds such as spicy, sour, bitter plant foods, and foods high in reactive oxygen species such as meat cooked in dry conditions at high temperatures	Fessler, 2003; Flaxman & Sherman 2000
Compensatory placental growth	Genetic conflict (3)	Mothers manipulated by fetuses to avoid foods with high energy density to favour placental growth	Foods with high energy density such as starches, sugars, oils, nuts, meat, and dairy	Huxley 2000
Gestational metabolic syndrome avoidance	Genetic conflict (3)	Mothers selected to avoid over-consuming foods associated with increased risk of gestational diabetes and preeclampsia	Foods with high glycemic indexes such as sugar, refined starches, some unprocessed starches, and very salty foods	Brown et al. 2013

Nutrient seeking, in response to nutrient deficits from aversions	Changes in energy budget (5)	Mothers selected to prioritize seeking out missing nutrients necessary for embryo/fetal development	Foods containing macro- and micro-nutrients otherwise not available in diet or in maternal tissue stores; Foods that meet similar nutritional requirements to aversive foods	Fessler, 2002
Procuring anti-oxidants	Oxidative stress (4)	Mothers selected to reduce oxidative stress caused by placental proliferation of reactive oxygen species	Foods high in anti-oxidants, especially fruits, vegetables, and fruit and vegetable juices	This paper

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858 **Table 2: Alphabetical list of food category bins with descriptions**

	Category	Description
1	*Bananas/plantains*	Any bananas or plantains, including both small sweet bananas and large plantains that require cooking
2	*Cassava*	Cassava
3	*Fish*	Any vertebral fish
4	*Imported Starches*	Any starchy foods not cultivated on Yasawa Island including rice, flours, noodles, sweets and sugars
5	*Locally-grown Starches*	Any starchy foods other than bananas/plantains, cassava, or imported starches such as yams, breadfruit, and taro
6	*Meat/dairy*	Terrestrial meat and animal products, such as beef, pork, chicken, or milk
7	*Non-fish aquatic*	Aquatic foods other than fish such as shellfish, turtles, squid, and freshwater eels
8	*Other fruits*	Fruits other than bananas/plantains, breadfruit, and limes
9	*Other vegetables*	Vegetables other than starchy or strongly-flavoured vegetables

10	*Spicy/ sour/ bitter plant foods*	spicy/ sour/ bitter plant products such as chili peppers, limes, curry, tea, coffee, and kava

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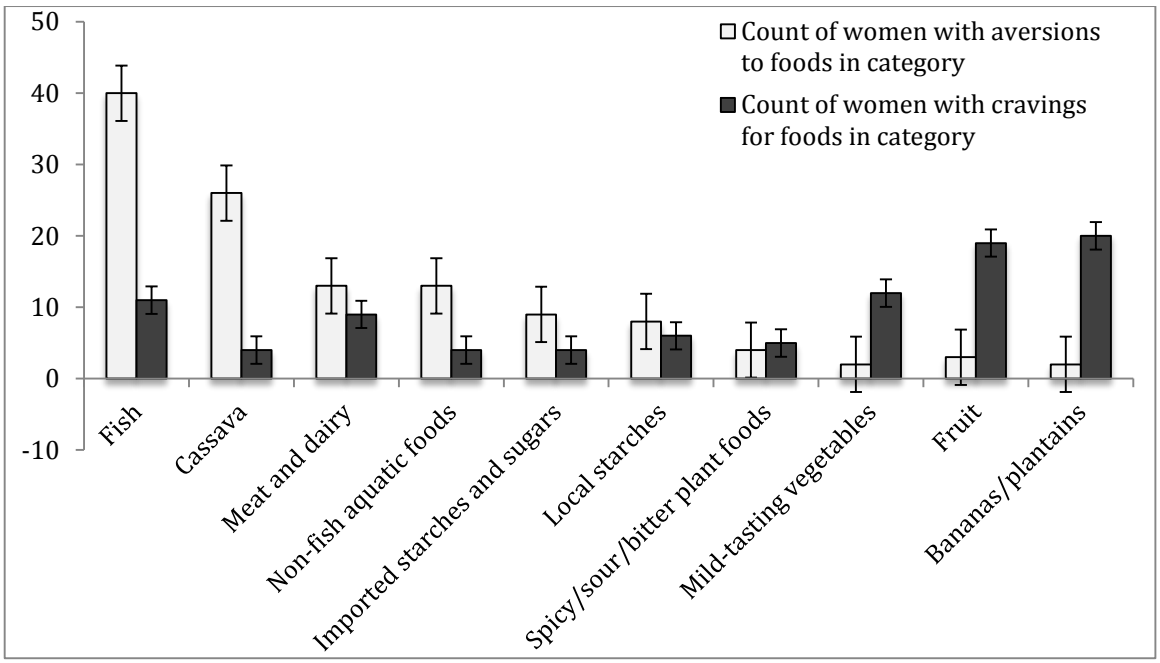
860 **Figure 1: Rates of aversions and cravings to specific food categories**



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862 **Table 3: Contingency table and χ^2 test results of impact of aversions on risk of developing a craving**

Test description	Aversions	Cravings		X^2 Result
Impact of specific aversions to animal foods on risk of developing specific cravings for animal foods		Crave specific animal foods	Do not crave specific animal foods	Simulated (1000 replicates) p-value
	Specific aversions to animal foods	23	3	0.012
	No specific aversions to animal foods	25	19	
Impact of specific aversions to cassava on developing specific cravings for bananas/ plantains		Crave bananas/ plantains	Do not crave bananas/ plantains	
	Specific aversions to cassava	18	8	0.004

	No specific aversions to cassava	11	33	
Impact of specific aversions to foods high in reactive oxygen species on developing specific cravings for antioxidant-rich foods		Crave anti-oxidant rich foods	Do not crave anti-oxidant rich foods	
	Specific cravings for meat	1	8	0.070
	No specific cravings for meat	29	32	

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Food Aversions and Cravings during Pregnancy on Yasawa Island, Fiji: Electronic Supplementary Materials, Online Resource 1

Human Nature

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[Online resource 1, section 1: Further details about characterizing the composition of the diet in the studied villages]

The diet data are based on interviews with the female household heads of 20 randomly sampled households from the village of Teci. Women were asked to recall in detail the foods that they had prepared for their households the previous day, and provide estimates of the quantities that they prepared. Some quantities were reported in mass (Kg or g), some in volume (cups or mL), and some in numbers of items (e.g. 1 onion, or "5 small fish").

We sought to characterize the proportion of macronutrients that each food mentioned by the participants contributes to the diets of the people of Yasawa. To standardize estimates across different kinds of quantitative measures and to characterize the macronutrient densities of the foods described, we used United States Department of Agriculture's Database for Standard Reference (USDADSF), a database that provides macro- and micro-nutrient nutritional profiles for a wide variety of foods. In cases in which a Fijian food type was not represented in the USDADSF, we substituted similar foods that were represented (the list of substitutions is available in the supplement of McKerracher et al. in press). The database allows queries and provides macronutrient estimates by mass, volume, or number of items, so we simply recorded the caloric yield, as well as the total grams of protein and the total grams of fat for each reported foodstuff. Then, we totaled the calories, fat, and protein yielded by each food for all meals in all 20 households. These were divided by the total calories, fat, and protein for all foods for all households to provide coarse estimates of the amounts of macronutrients each type of food contributes to the diet on Yasawa Island. These estimates for the most important food categories (listed alphabetically) are summarized in Table ESM1.

Table ESM1: Macronutrient contributions to overall diet of 10 major food categories regularly consumed by men, women, and children of Yasawa Island

Food category (specific foods mentioned by women from this category)	**% of total diet calories**	**% of total diet fat (g)**	**% of total diet protein**
Cassava (cassava)	47	6	9
Fish (*boisa*, *yaluya*, *sabutu*, *silasila*, tinned tuna, *yalewa*)	7	10	49

Local starches other than cassava (*usuvanua*, *uto*, *vudi*, yams)	3	1	0
Imported starches and sugars (flour, sugar, rice, noodles, biscuits)	29	12	16
Meat/ dairy (eggs, tinned beef, lamb)	1	2	4
Non-fish aquatic foods (mollusks – *kadrei*, *kawai*, *matakarawa*, octopus, *vasua*)	3	2	15
Oil (oil, coconut cream)	2	12	0
Other fruit (coconut, mango, malay apple, pawpaw, pineapple)	8	57	3
Other vegetables (*bele*, eggplant, taro leaves, tomatoes)	0	0	0
Spicy/ sour/ bitter plant foods (tea, onions, curried dahl, curry powder)	1	0	3

[Online Resource 1, section 2: Further details about the participants, pregnancy, and demography]

The 70 women that participated in the pregnancy interview ranged in age from 21 to 75, with a mean age of 41. Assuming an age of reproductive cessation of 45, at least 26 women were post-reproductive when interviewed, and the total fertility rate for this subsample was 4.14. In a largely overlapping sample of 76 women who were interviewed about their reproductive histories, late pregnancy or perinatal mortality was reported to occur five times out of 268 known pregnancies, or ~19 per 1,000 live births. The rate of early pregnancy loss is unknown for this population. Maternal mortality rate is also unknown for the study population.

[Online Resource 1, section 3: Further details about comparing pregnancy-related aversions and cravings data yielded by the open-ended questions with data yielded by the checklist questions]

In addition to free-listing aversions, taboos, and cravings, the interviewers provided a list of 17 specific food categories and asked each of the participants identify all of the foods on the list as aversive to her during a past pregnancy or not, thought to be taboo for pregnant women or not, and craved by her during a past pregnancy or not. The original list was designed to identify whether specific taxa that are likely to contain high levels of a particular marine toxin were considered especially taboo but, for the purpose of this study, we've collapsed some of these narrow taxonomic categroies into 10 slightly broader categories. The 10 classifications on the list were: cassava, dairy, fish, fruit, meat, shellfish, sweets, spicy foods, vegetables, and yams.

The rank-ordering of whether a food was highly aversive or highly craved appears to be broadly similar between the freelist responses and the questionnaire responses. In both

datasets, fish and cassava appear to be highly aversive, meat and shellfish appear to be moderately aversive, and fruits and bland vegetables are rarely aversive (see Table ESM2). Furthermore, the proportion of women that free-listed aversions to a specific food category was highly correlated with the proportion of women that reported checklist aversions to that category ($r=0.91$, $p<0.001$). With respect to cravings, fruit, vegetables, and fish appear to be the most craved items in both lists, and all other food categories are only moderately craved (See Table ESM3). The proportions of the women with free-listed cravings to particular food categories correlate with the proportions of the women with checklisted cravings for those categories ($r=0.51$, $p<0.001$).

Table ESM2: Comparison of rates of reported pregnancy-related food aversions from free-list questions and checklist questions. Values above 30% for the freelist data and above 50% for the checklist data were considered high. Values between 10% and 29% or between 20% and 49% for the freelist and checklist data, respectively, were scored as moderate. Foods categories that were freelisted as aversive by less than 9% of women or that were checked as aversive by less than 19% of women were viewed as low in aversiveness. Ranking discrepancies between the two interview methods are highlighted in grey.

Food category	Freelist % of population (ranking)	Checklist % of population (ranking)
Cassava	35% (high)	51% (high)
Dairy	1% (low)	20% (moderate)
Fish	57% (high)	64% (high)
Locally-grown starches other than cassava/ "yams"	11% (moderate)	20% (moderate)
Imported starches/ "sweets"	12% (moderate)	20% (moderate)
Meat	18% (moderate)	39% (moderate)
Non-fish aquatic foods/ "shellfish"	17% (moderate)	34% (moderate)
Other fruits (excludes lime, bananas/ plantains, breadfruit)	3% (low)	10% (low)
Other vegetables/ "vegetables" minus tea	3% (low)	14% (low)
Spicy/ sour/ bitter plant foods/ "spicy" plus tea	7% (low)	36% (moderate)

Table ESM3: Comparison of rates of reported pregnancy-related food cravings from free-list questions and checklist questions. For cravings, any values above 20% were considered high for the freelist data and any values above 90% were considered high in the checklist data. Values between 9% and 19% were ranked as moderate for the freelist data and values between 50% and 89% were ranked as moderate for the checklist data. Ranking discrepancies between the two interview methods are highlighted.

Food category	Freelist % of population (ranking)	Checklist % of population (ranking)
Cassava	6% (low)	70% (moderate)
Dairy	1% (low)	79% (moderate)
Fish	16% (moderate)	64% (moderate)
Locally-grown starches other than cassava or bananas and plantains (classed here with fruit)/ "yams"	9% (moderate)	79% (moderate)
Imported starches/ "sweets"	6% (low)	40% (low)
Meat	13% (moderate)	78% (moderate)

Non-fish aquatic foods/ "shellfish"	6% (low)	81% (moderate)
Other fruits (excludes lime, breadfruit; includes bananas/ plantains)	43% (high)	94% (high)
Other vegetables/ "vegetables" minus tea	17% (moderate)	90% (high)
Spicy/ sour/ bitter plant foods/ "spicy" plus tea	7% (low)	47% (low)

Despite the substantial overlap between the two methods of assessing aversions and cravings, there are also some obvious discrepancies between them. Specifically, the questionnaire data consistently presents higher numbers of women with aversions to or cravings for a particular food than the parallel count for the freelist data, suggesting that women were regularly omitting or forgetting items from their lists. Dairy stands out as the most under-reported category, with only one woman spontaneously reporting a dairy aversion and only one woman spontaneously reporting a dairy craving. In contrast, the questionnaire data indicate that non-trivial portions of the sample were either averse to or craved dairy. Similar but less extreme patterns characterize aversions to spicy foods and cravings for cassava. It is currently unclear if the under-reporting indicates that some classes of food such as dairy are simply encountered less frequently and thus are less likely to be recalled by the women of Yasawa Island as aversive or craved than others, or if they are actually less cognitively salient for some other reason. Regardless, despite this problem with the freelist data, the questionnaire data cannot be relied on as the sole or even the principal data source for this particular study because of our inclusion of the cravings data. Food cravings are easily elicited by auditory cognitive primes or other social primes (e.g. Fedoroff et al. 2003; Sobik et al. 2005) in a way that appears not to be the case with food aversions, which are generally acquired through individual learning and are elicited through taste (Bernstein 1994). As such, the checklisted cravings, cued through the questionnaire, may substantially inflate the rates at which women actually experienced genuine, specific cravings for particular food types. An additional problem with the checklist data is that they fail to capture at least three categories of food that emerge endogenously from the open-ended questions. Specifically, the following three categories emerged from the freelist data: 1) several women reported aversions to imported starchy foods such as rice, noodles, biscuits, flour, and roti (a kind of flatbread) and this class of aversions is not encapsulated by any category in the original questionnaire list; 2) a large proportion of women reported cravings specifically for bananas and/ or plantains, which are subsumed under the category "fruit" in the questionnaire data, but appear to occupy a very different role in the pregnancy diet than other, less energetically dense fruits because several women said that they craved fruits *and* bananas/ plantains; 3) some women mentioned that they found tea or kava aversive, and these beverages do not map directly onto any of the questionnaire categories. We also had the additional problem of interpreting notes in the questionnaire data that indicate that lime is sometimes classed as a fruit, sometimes as a "spicy food" and sometimes as both, making it difficult to assess how many women actually had genuine fruit aversions or cravings or whether most of the reported aversions to the category "fruit" in the questionnaire may reflect lime aversions. Coconuts, sometimes viewed as taboo, were also difficult to classify, although they were rarely cited

as aversive or craved in the freelist data, so we binned them with fruit. Finally, the questionnaire data do not shed light on whether women were averse to or craved particular forms of food preparation methods, while the freelist data indicate that whether a food is boiled, fried, grilled, or raw impacts the extent to which it is avoided or desired during pregnancy.

Given these problems with the questionnaire data, we decided to focus our analyses on the freelist data, although we have carried out slightly different analyses with the checklist data pertaining to aversions elsewhere (McKerracher et al. in press).

[Online Resource 1, section 4: Summary statistics for rates of aversions and cravings]

Tables ESM4 and ESM5 present the summary statistics regarding rates of food aversions and food cravings per food category for the women of the Yasawa Island. The values represent the percentage of women from the full sample that reported experiencing an aversion or a craving for a particular food category when given the opportunity to freelist. Table ESM4 shows overall prevalence rates of aversions and cravings. Table ES5M shows prevalence rates for specific food categories.

Table ESM4: Overall prevalence of aversions and cravings among pregnant Yasawan women

Food category	Number of aversions (% of full sample)	Number of cravings (% of full sample)
All foods	3 (4%)	14 (20%)
No foods	20 (29%)	0 (0%)
Some foods	47 (71%)	56 (80%)

Table ESM5 Rates at which women from Yasawa Isalnd developed novel aversions and novel cravings to specific categories of food.

Food category	Number of aversions (% of full sample)	Number of cravings (% of full sample)
Bananas/ plantains	0 (0%)	20 (29%)
Cassava	26 (37%)	4 (6%)
Fish	40 (57%)	11 (16%)
Locally-grown starches	8 (11%)	4 (6%)
Imported starches	9 (13%)	4 (6%)
Meat/ dairy	14 (20%)	9 (13%)
Non-fish aquatic	13 (19%)	4 (6%)
Other fruit	1 (1%)	19 (27%)
Other vegetables	2 (3%)	12 (17%)
Spicy/sour/bitter vegetables	5 (7%)	5 (7%)

References

Bernstein, I. L. (1994) Development of food aversions during illness. Proceedings of the Nutrition Society, **53**, 131-137.

Fedoroff, I., Polivy, J. & Peter Herman, C. (2003) The specificity of restrained versus unrestrained eaters' responses to food cues: general desire to eat, or craving for the cued food? Appetite, **41**, 7-13.

McKerracher, L., Collard, M. & Henrich, J. (in press) The expression and adaptive significance of pregnancy-related nausea, vomiting, and aversions on Yasawa Island, Fiji. Evolution and Human Behavior, **http://dx.doi.org/10.1016/j.evolhumbehav.2014.09.005**.

Sobik, L., Hutchison, K. & Craighead, L. (2005) Cue-elicited craving for food: a fresh approach to the study of binge eating. Appetite, **44**, 253-261.