Hum Nat
DOI 10.1007/s12110-016-9262-y

Food Aversions and Cravings during Pregnancy on Yasawa Island, Fiji

Luseadra McKerracher[1] · **Mark Collard**[1,2] · **Joseph Henrich**[3]

Abstract Women often experience novel food aversions and cravings during pregnancy. These appetite changes have been hypothesized to work alongside cultural strategies as adaptive responses to the challenges posed by pregnancy (e.g., maternal immune suppression). Here, we report a study that assessed whether data from an indigenous population in Fiji are consistent with the predictions of this hypothesis. We found that aversions focus predominantly on foods expected to exacerbate the challenges of pregnancy. Cravings focus on foods that provide calories and micronutrients while posing few threats to mothers and fetuses. We also found that women who experience aversions to specific foods are more likely to crave foods that meet nutritional needs similar to those provided by the aversive foods. These findings are in line with the predictions of the hypothesis. This adds further weight to the argument that appetite changes may function in parallel with cultural mechanisms to solve pregnancy challenges.

Keywords Pregnancy · Diet · Aversions · Cravings · Behavioral ecology · Fiji

Electronic supplementary material The online version of this article (doi:10.1007/s12110-016-9262-y) contains supplementary material, which is available to authorized users.

✉ Luseadra McKerracher
ljm8@sfu.ca

[1] Department of Archaeology and Human Evolutionary Studies Program, Simon Fraser University, EDB 9635, 8888 University Drive, Burnaby, BC V5A 1S6, Canada

[2] Department of Archaeology, University of Aberdeen, UK. St Mary's Building, Elphinstone Road, Aberdeen, Scotland AB24 3UF, UK

[3] Department of Human Evolutionary Biology, Harvard University, Peabody Museum, 11 Divinity Avenue, Cambridge, MA 02138, USA

Published online: 14 May 2016

In this paper, we report new data regarding the development of novel food aversions and cravings during pregnancy in an indigenous population from Yasawa Island, Fiji. We show that these data are consistent with the hypothesis that appetite changes in pregnancy represent an adaptive strategy for dealing with challenges to maternal and offspring fitness posed by gestation. That is, the data suggest that pregnant women avoid eating foods likely to increase risks of fetal morbidity and/or mortality. They also seek to eat foods likely to improve fetal health outcomes, and they do so in a way that appears to compensate for possible nutritional losses related to food avoidances.

To a much greater extent than other life history stages, pregnancy presents an opportunity for strong selective processes to operate on both genes and culture (Brown et al. 2013). For mothers and offspring, pregnancy poses at least four major immunological, endocrinological, metabolic, and developmental challenges. These challenges are as follows:

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 (Fessler 2002; Flaxman and Sherman 2000; Svensson-Arvelund et al. 2013).
2) **Embryo Tissue Differentiation:** Embryonic tissues differentiate and organogenesis occurs in early pregnancy. Developmental insults from illness, insufficient access to requisite nutrients, or exposure to chemical toxins during this phase can have substantial downstream negative effects on offspring phenotype (Langley-Evans 2006; Myatt 2006; Rillamas-Sun 2010).
3) **Genetic Conflict:** Pregnancy requires a mother and her offspring to share maternal resources, but the interests of mothers and offspring differ because they share only ~50% of their genes (Haig 1993; Trivers 1974). Consequently, offspring can be expected to demand more energetic investment than mothers are willing to supply. This conflict can negatively impact maternal metabolic function and offspring health and survivorship if it does not result in the equitable partitioning of resources (Crespi 2010, 2011; Crespi and Badcock 2008; Das et al. 2009; Haig 1993). Unchecked fetal manipulation of maternal endocrinology can dangerously elevate maternal blood pressure and rates of protein excretion (preeclampsia). It can also impair sugar absorption and elevate circulating sugar levels (gestational diabetes mellitus).
4) **Changes in Energy Budget and Nutrient Requirements:** Support of a fetus increases a mother's energy and nutrient requirements (Dufour and Sauther 2002; Fessler 2002). 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 to secure and mobilize energy and nutrients. Availability of certain micronutrients during early pregnancy—including folate, iodine, iron, long-chain polyunsaturated fatty acids, vitamin A, and vitamin D—via maternal stores or diet affects fetal survivorship and developmental outcomes (e.g., Bath et al. 2013; Forbes 2014; Lee et al. 2004; Maconochie et al. 2007).

All of these challenges affect and/or are affected by diet and eating behaviors. At the same time, eating presents its own set of adaptive challenges throughout the life course

(Sherman and Flaxman 2001). Many edible compounds necessary for growth, development, and body maintenance are toxic if ingested in amounts above a size- and development-stage-specific dose threshold (Gerber et al. 1999). Furthermore, many plants have evolved to produce toxic compounds to reduce risk of exploitation by fungi, parasites, pathogens, and predators (Billing and Sherman 1998; Fessler 2002; Flaxman and Sherman 2000, 2008; Sherman and Flaxman 2001; Sherman and Hash 2001). Such compounds can disrupt or even shut down cellular function in humans. Lastly, eating provides food-borne pathogens ready access to the bloodstream (Sherman and Flaxman 2001).

Evidence suggests that humans have evolved physiological, psychological, and cultural solutions to the challenges associated with eating (Eaton and Konner 1985; Patil and Young 2012). With respect to physiology, ingestion of biochemical toxins and/or high levels of food-borne pathogens can trigger a number of reactions, most notably vomiting and diarrhea, which facilitate the rapid expulsion of toxic or contaminated food items (Flaxman and Sherman 2000). Psychologically, we experience appetite sensations such as the development of aversions to foods previously associated with nausea, vomiting, and/or diarrhea, and the development of cravings for foods that contain difficult-to-obtain nutrients (Patil and Young 2012; Williams and Nesse 1991). These appetite sensations affect behavior: aversions have been found to be associated with the avoidance of particular food items while cravings have been found to be associated with the targeting of particular food items (Drewnowski 1997; Sclafani 1997). Culturally, many human populations possess food taboos—prohibitions against eating certain foods—that focus preferentially on foods especially likely to pose health risks (Fessler and Navarrete 2003). Moreover, many populations heat foods to temperatures sufficiently high to denature bacterial proteins and/or add spices that contain antimicrobial compounds at levels sufficient to slow the proliferation of food-borne pathogens (Billing and Sherman 1998; Sherman and Flaxman 2001; Sherman and Hash 2001). Also in the cultural realm, particular food items and recipes are often associated with desirability, and such food items frequently contain difficult-to-access essential nutrients (Rozin and Vollmecke 1986).

Given that selection is expected to be particularly strong during pregnancy and that human diets appear to have been shaped in part by both genetic and cultural evolution to 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 food-related challenges of pregnancy. Reflecting this line of reasoning, a number of complementary hypotheses have been put forward 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 the challenges to which they relate can be summarized as follows (see also 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 especially likely to contain pathogens or chemical toxins (Fessler 2002; Flaxman and Sherman 2000; Hook 1978, 1980; Profet 1988, 1992). The development of these aversions coincides with the gestational phase during which pregnant women experience adaptive immune suppression and during which embryo tissue differentiation occurs (Fessler 2002; Flaxman and Sherman 2000). This phenomenon

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 differentiation (2)	Mothers selected to avoid chemical toxins in food to prevent fetal teratogenesis	Aversions to 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 differentiation (1,2)	Mothers selected to avoid disease-causing microbes and chemical toxins in food to prevent maternal illness and fetal developmental insult	Aversions to foods with high spoilages rates such as fish and meat, foods high in anti-microbial chemical compounds such as spicy, sour, bitter plant foods	Fessler 2002; Flaxman and Sherman 2000
Compensatory placental growth	Genetic conflict (3)	Mothers manipulated by fetuses to avoid foods with high energy density to favor placental growth	Aversions to 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	Aversions to 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	Cravings for 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

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 (Fessler 2002).

The **compensatory placental growth hypothesis** proposes that pregnancy-related food aversions result from fetal manipulation of maternal physiology such that mothers are motivated to avoid energy-dense foods. Counterintuitively, 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 we will 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 to secure relatively high levels of maternal investment (Haig 1993, 1999). According to the hypothesis, mothers may also have evolved various counter-adaptations to reduce the risk of developing these conditions.

The **nutrient-seeking hypothesis** contends that pregnancy-related cravings motivate women to find and eat foods containing the energy, macronutrients, and micronutrients that are essential to fetal development (Hook 1978, 1980; Tierson et al. 1985). Fessler (2002) has proposed an important addendum to this hypothesis. He suggests that pregnant women may have particular propensities to seek nutrients depleted in or missing from their diets because of food aversions and vomiting. In other words, Fessler argues for a functional link between cravings and aversions.

These four hypotheses are not mutually exclusive. All the challenges of pregnancy may play a role in driving within- and among-population variation 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 and socially transmitted information about foods that may improve maternal and/or fetal health outcomes. Despite these linkages, few, if any, previous empirical studies have treated food aversions and food cravings of pregnancy (and/or their cultural equivalents) as an adaptive complex that coevolved to solve the suite of ecological and physiological challenges imposed by gestation. In the present paper, we aim to do just that. Specifically, we investigate whether pregnancy-related aversions and cravings reported by indigenous women from Yasawa Island, Fiji, are consistent with the idea that aversions and cravings during pregnancy are adaptive. Our formal evaluations focus particularly on Fessler's extension to the nutrient-seeking hypothesis—the idea that cravings not only serve to motivate pregnant women to seek out crucial and/or difficult-to-obtain nutrients but also motivate women to compensate for nutrient losses related to aversions.

Population, Data, and Methods

The data we analyze derive from interviews with 70 women about appetite sensations during pregnancy. These data were collected as part of an ongoing research project led by JH on social organization, ecology, life history, and culture on Yasawa Island, Fiji.

For several years, JH and his team have gathered information from the people of Yasawa about local subsistence economy, diet, food taboos, reproductive histories and demography, and cultural learning and transmission (Broesch et al. 2014; Henrich and Broesch 2011; Henrich and Henrich 2010; Kline et al. 2013; McKerracher et al. 2015).

Yasawa Island is on the northwest end of the Fijian archipelago. The climate is warm year-round and is characterized by a wet season and a dry season. The soils are sandy and dry, but sufficient to produce a variety of root and fruit crops (see data supplement for Henrich and Henrich 2010).

The people of Yasawa are primarily small-scale fisher-farmers. Men in these communities fish and maintain garden plots. 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 the Yasawa Islanders are predominantly local. Cassava provides the majority of calories, although yams, plantains, breadfruit, and imported wheat and sugar are also calorically important. 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 gardens along with some imported dairy products likely offer a variety of micronutrients. Commonly consumed beverages include tea and *yaqona* (kava), a drink prepared from a root native to Oceania that has sedative properties. Information on how core dietary items were ranked relative to one another with respect to macronutrient density is available in the Electronic Supplementary Materials (ESM, section 1).

Women from three different villages were interviewed. All of them had at least one child at the time of the interview (see ESM, 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; we do not report the taboo responses here because those responses have been presented elsewhere (Henrich and Henrich 2010). In addition, each woman was asked about the timing of appetite-suppressing symptoms of pregnancy; as with the answers to the food taboo questions, these data have already been reported (McKerracher et al. 2015) so we do not present the results in detail here. We do note, however, that these symptoms generally tend to peak in the first 3 months of pregnancy. We did not collect data on the timing of pregnancy-related food cravings on Yasawa, but evidence from other populations suggest that, as with aversions, cravings generally peak during pregnancy's first trimester (Flaxman and Sherman 2000). 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 ESM (section 3).

We coded the refined freelist responses into ten categories. These categories are listed alphabetically within three super-categories (animal-based foods; starchy, calorie-dense plant-based foods; and all other plant foods) in Table 2.

Table 2 Alphabetical list of food category bins with descriptions

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

After coding responses, we carried out two sets of analyses. First, we created bar graphs that represent the frequencies at which women spontaneously reported foods in a given category to be aversive and/or craved. Second, using Fisher's exact tests, we tested the prediction of the nutrient-seeking hypothesis that women who likely experienced nutrient losses due to aversions were more likely than other women to develop cravings for foods that could compensate for those losses. Analyses were carried out in R (R Development Core Team 2008).

Results

The overall rates of aversions and cravings from the freelist responses are summarized in Table ESM4. We present the food category-based aversions and cravings data used in the first set of analyses in Fig. 1 as well as in Table ESM5.

Regarding aversions, we found that 50 women (71% of the sample) reported developing at least one novel aversion during past pregnancies while 20 women (29% of the sample) reported having experienced no aversions. Three of the 50 women with aversions (4% of the sample) said they disliked all foods during the early phase of pregnancy.

The more detailed aversions data presented in Fig. 1 focus on the 47 women who experienced aversions to specific types of foods. For these women, fish was the most commonly aversive food (41 women or 87%), followed by cassava (26 women or

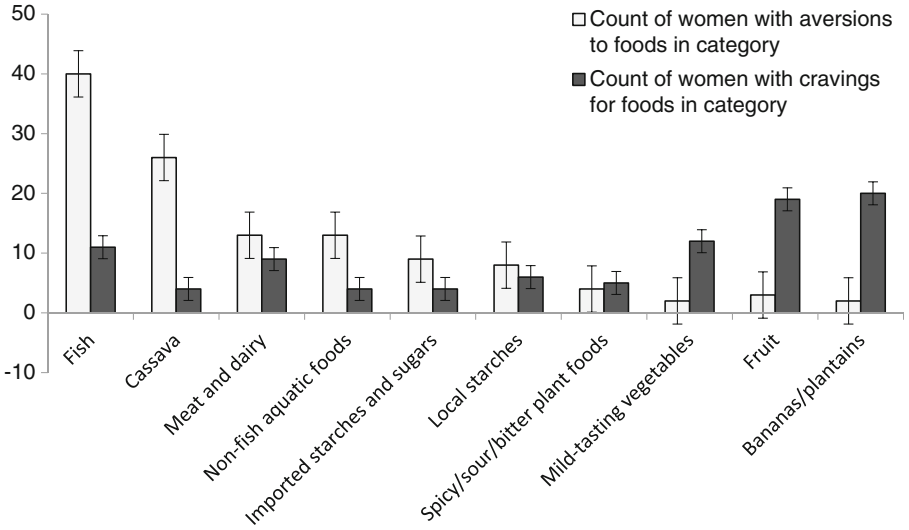

Fig. 1 Rates of aversions to and cravings for specific food categories

55%), meat (13 women or 28%), non-fish aquatic foods (13 women or 28%), imported starches (9 women or 19%), locally grown starches (8 women or 17%), and, rarely, spicy/sour/bitter-tasting vegetables (4 women or 9%). Bananas/plantains and other fruits and vegetables generally were 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. The remaining 56 women identified more specific food cravings. Among these women, the most frequently identified category of craved foods was bananas/plantains (20 women or 36%), followed by other fruits, especially mangos (19 women or 34%); other vegetables, especially leafy greens (12 women or 21%); fish (11 women or 20%); and meat (9 women or 16%). Foods from all other 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 not often craved and more craved foods were not often aversive (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. We note that, despite this general pattern at the population level, for many individual women, having an aversion to one particular food within a food category did not prevent her from also having a craving for a different food within that same category or super-category.

Table 3 summarizes the results of the second set of analyses in which we used Fisher's exact tests to assess whether nutrient losses from aversions affect the foci for cravings. We found that women who 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. We also found that women without specific aversions were much more likely than other women to report non-specific cravings. Specifically, women with aversions to particular kinds of animal foods were

Table 3 Contingency table and Fisher exact test results of impact of aversions on risk of developing a craving

Test description	Aversions	Cravings		Fisher's Exact *p*
Impact of aversions to specific animal foods on risk of developing cravings for specific animal foods		Craves animal foods	Does not crave animal foods	0.004
	Averse to one or more specific animal foods	23	3	0.004
	No specific aversions to animal foods	25	19	
Impact of aversions to cassava on developing cravings for bananas/ plantains		Crave bananas/ plantains	Do not crave bananas/ plantains	
	Averse to cassava	13	13	0.003
	No specific aversions to cassava	7	37	
Impact of having no specific aversions on developing only general cravings		Any specific cravings	Only general cravings	
	Any specific aversions	45	3	0.000
	No specific aversions	10	12	
Impact of having no specific aversions on developing cravings for fruit and/ or mild-tasting vegetables		No specific cravings for fruit and/or mild-tasting vegetables	Craves fruit and/or mild-tasting vegetables	
	Any specific aversions	25	23	0.019
	No specific aversions	5	17	

more likely than other women to report cravings for other animal foods ($p = 0.0004$). These craved foods conspicuously differ from the animal foods on which their aversions focus. Women with aversions to staple dietary starches, especially cassava, were relatively likely to report cravings for bananas/plantains ($p = 0.003$). Women without specific aversions were more likely than women with specific aversions to report either no specific cravings (i.e., they reported craving "all foods": $p = 0.000$) or cravings for fruit and/or mild-tasting vegetables ($p = 0.019$).

Discussion

The evidence reported here indicates that pregnancy-related food aversions and cravings among the women of Yasawa Island are prevalent and strongly patterned. Most of the women reported developing aversions during early pregnancy to particular foods that they would normally enjoy, and all of the women 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 starchy plant-based foods. Yasawan women most often reported craving bananas/plantains followed by less-starchy fruit and mild-tasting vegetables. Women who experienced specific aversions were more likely than other women to report cravings for foods that would replace nutrient losses caused by those aversions. Women who did not report experiencing aversions were especially likely to report only general cravings for "all foods" or to report cravings for fruit and/or mild-tasting vegetables.

Although the nutrient-seeking hypothesis was the only adaptive hypothesis for which we developed and evaluated predictions, the patterns in our data are generally consistent with the expectations of several adaptive hypotheses proposed to explain why food aversions and cravings coincide and why both aversions and cravings occur at the same time as four of the physiological challenges posed by early pregnancy. Taking the three super-categories (animal-based foods, starchy plant-based foods, and all other plant foods) in turn, we briefly discuss how rates of aversions to and cravings for different types of foods relate to the hypotheses and their general predictions and to the wider literature on adaptive explanations for pregnancy-related cravings and aversions.

Aversions to and Cravings for Animal-Based Foods

Animal-based foods, especially fish, represent the most common sources of novel aversions. Foods from this super-category were also reported as craved items by non-trivial numbers of women in the Yasawa Island sample.

One plausible explanation for the high rate at which women reported animal products (especially fish) as aversive derives from the maternal-embryo protection hypothesis. Several 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 (Fessler 2002; Fessler et al. 2005; Flaxman and Sherman 2000; see also Steinmetz et al. 2012; Weigel et al. 2011). Animal foods are especially salient

sources of pathogens on Yasawa 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. In line with this reasoning, in a previous study using checklist data from women from Yasawa Island, we found that the pathogenicity and/or chemical toxicity of a food category was the most reliable predictor of whether women were likely to develop novel aversions to it, in keeping with the predictions of the maternal-embryo protection hypothesis (McKerracher et al. 2015).

That many Yasawan women report cravings for animal-based foods is in keeping with the predictions of the nutrient-seeking hypothesis and may indicate that the women in question are not in a position to afford the nutrient debits associated with excluding all or most animal foods from their diets. Consistent with this idea, women with aversions to fish were nearly twice as likely to have specific cravings for other kinds of animal-based foods, such as specially prepared fish, meat/dairy, or particular species of shellfish, than women without fish aversions (Table 3). In addition to contributing substantial energy and protein to the Yasawan diet (Table ESM1), animal-based foods are sources of several micronutrients crucial to early fetal development that cannot be synthesized by mothers, may not be available in sufficient quantities in maternal repositories, and cannot be obtained from plant-based foods. In particular, as mentioned previously, deficiencies in some fatty acid chains, folate, iodine, iron, and vitamin D in early pregnancy can reduce fetal survivorship prospects or increase risks of impaired development (Bath et al. 2013; Forbes 2014; Lee et al. 2004; Maconochie et al. 2007). These micronutrients are best obtained through consumption of fish and/or other animal-based foods (e.g., Biesalski 2005; Bonham et al. 2008). Thus, in line with the nutrient-seeking hypothesis, women who face the problem of certain micronutrient shortages because of aversions to animal foods may be motivated by cravings to focus on securing these nutrients from the few animal-based foods they do not find aversive.

Aversions to and Cravings for Starchy Plant-Based Foods

More than half of the Yasawan women with specific aversions reported an aversion to at least one starchy plant-based food, with cassava being the most frequently targeted by far. Such aversions are surprising for at least two reasons. First, starchy plant-based foods represent the main source of calories on the island. Second, staple starches tend to be among the least aversive foods in the majority of other populations studied to date—mostly European or Euro-American populations (Flaxman and Sherman 2000). Less surprisingly, and in keeping with the findings from other populations, this starchy plant-based food super-category also contains the most frequently craved food item among pregnant women from Yasawa Island—namely, bananas/plantains.

The maternal embryo protection hypothesis supplies a potential explanation for the high rates of pregnancy-related aversions 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). Cyanide levels may be especially high in cassava cultivated in dry, sandy soils such as those of Yasawa (e.g., Cadavid et al. 1998; El-Sharkawy 2006). Anecdotally, several women in the Yasawa sample reported that the smell and/or taste

of cassava was 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 reducing the risk of fetal exposure to the chemical toxin cyanide as a consequence. In this population, a generalized bitter taste/smell cue is a more plausible mechanism than a specific cyanide detection mechanism, given that cassava was only introduced to Oceania in the mid 1800s (Bradbury et al. 2013) and has only been the dominant staple since the mid 1900s (Thaman 1990).

The gestational metabolic syndrome avoidance hypothesis and the compensatory placental growth hypothesis both predict that pregnant women may develop aversions to nontoxic starchy foods. However, we think the gestational metabolic syndrome avoidance hypothesis offers a better explanation for aversions to nontoxic starches than the compensatory placental growth hypothesis, at least in this population. We question the compensatory placental growth hypothesis's cogency in this context because it predicts that all energy-dense foods should be aversive to pregnant women, and we find little evidence to support this (see Tables ESM1 and ESM5; see also McKerracher et al. 2015). Rather, consistent with the gestational metabolic syndrome avoidance hypothesis, aversions to energy-dense foods among Yasawan women focus disproportionately on staple starches.

As Brown et al. (2013) suggest, women may have evolved adaptations to reduce the risk of expressing extreme and pathological gestational metabolic symptoms, including symptoms of gestational diabetes and/or preeclampsia. One such set of adaptations that appears to characterize populations with long histories of cereal farming and energy surplus (Brown et al. 2013) involves genetic selection against alleles associated with metabolic syndromes (Ségurel et al. 2013). Another evolved strategy for populations without long histories of cereal farming may involve developing aversions to foods implicated in the etiology of gestational metabolic syndromes. The aversions strategy may offer a flexible solution, contingent on current energy availability, 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 owing either to unavailability of cereal grains and starches in the diet or to intense and regular famine cycles. Consistent with this notion, high rates of pregnancy-related aversions to some kinds of starchy foods have recently been observed in several populations without long histories of consuming refined sugars and starches, such as the Datoga, the Turkana (Young and Pike 2012), and the Pemba Island peoples of East Africa (Steinmetz et al. 2012). Similarly, among Yasawa women, 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 (Fig. 1).

Regarding starch cravings, the nutrient-seeking hypothesis may account for the relatively high rates of cravings for specific forms of such foods. 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 (Fessler 2002). Being underweight nearly doubles the risk of spontaneous abortion before 12 weeks gestation (Maconochie et al. 2007). Severe calorie restriction during pregnancy is also associated with reduced neonatal and early

childhood survivorship as well as with increased risk of developing noncommunicable metabolic diseases in both childhood and adulthood (Dulloo et al. 2006; Gluckman and Hanson 2004; Godfrey et al. 2010; Hales and Barker 1992; Langley-Evans and McMullen 2010; Patti 2013; Wells 2009; Wood-Bradley et al. 2013). Yasawan women may partially solve this problem of energy loss from cassava and other starch aversions by developing cravings for bananas/plantains, which offer energy while posing no toxicity risks and only relatively low hyperglycemia risks. As predicted by the nutrient-seeking hypothesis, banana/plantain and starch cravings were common in the sample as a whole (Fig. 1) and were especially common in the subsample of women with cassava aversions (Table 3). 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 calorie loss associated with not consuming staple crops. We also note that 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 relatively common for women with no specific aversions (Table 3). This pattern suggests that women with aversions to staple starches may prioritize meeting energy requirements before meeting other nutritional needs, which is not the case for women who are well supplied with energy from cassava and other starchy plant-based staples.

Aversions to and Cravings for Fruits and Vegetables

Few women from Yasawa Island reported aversions to fruits or mild-tasting vegetables but many women reported cravings for foods from these food categories. Spicy/sour/bitter plant foods were identified by a small number of women as aversive and were rarely craved.

The low frequency of aversions to fruits or vegetables 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, and gestational metabolic syndromes. Since these foods pose few morbidity or mortality risks to pregnant women or to fetuses relative to other foods, adaptive hypotheses for pregnancy-related food aversions predict that women should rarely develop aversions to fruits and vegetables. Similarly low rates of fruit and vegetable aversions are reported for other previously studied populations (e.g., Flaxman and Sherman 2000; Olusanya and Ogundipe 2009; Steinmetz et al. 2012; Weigel et al. 2011, but see Placek and Hagen 2015 for a recent counterexample).

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

cues about the possible chemical toxicity of these plant foods and are thus developing aversions to them (Flaxman and Sherman 2000; Sherman and Flaxman 2002).

Turning to cravings for fruits and mild-tasting vegetables, as mentioned above, foods from this super-category were among the most frequently reported pregnancy-related cravings among the women of Yasawa Island. Such cravings were especially prevalent among women who did not freelist any specific food aversions (Table 3). The findings that fruit and mild-tasting vegetables are among the most frequently craved food items in pregnancy, particularly among women without specific food aversions, is consistent with the nutrient-seeking hypothesis. This hypothesis holds, in part, 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). The hypothesis also suggests that cravings help women to prioritize consuming particular nutrients over others. For energetically undernourished women, appetite-suppressing symptoms of early pregnancy may not be affordable, or loss of desire for energy-dense foods such as starchy staples may not be affordable (Holland and O'Brien 2003; Pike 2000). However, for women who are relatively well-nourished, such as women from Yasawa Island without strong pregnancy-related aversions, securing energy during the first trimester may be a relatively low priority whereas securing limited and easily depleted vitamins that can be found in fruits and vegetables, such as vitamin A and folate, may be a relatively high priority. Consistent with this reasoning, similar patterns have been documented for well-nourished populations from Europe and North America (Flaxman and Sherman 2000), South America (Weigel et al. 2011), and Sub-Saharan Africa (Steinmetz et al. 2012). Thus, women may develop cravings for fruits and vegetables because such cravings motivate them to seek out key micronutrients when the demands of early fetal development overtax maternal stores of such resources.

Implications of Pregnancy-Related Food Aversions and Cravings for Human Evolution and Avenues for Future Research

These findings regarding focal categories for food aversions and cravings among Yasawan women, taken together with previous work in the same population on pregnancy food taboos (Henrich and Henrich 2010) and on nausea and vomiting of pregnancy (McKerracher et al. 2015), have a number of implications for understanding human ecology and evolution and suggest several 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 foods. Pregnancy is a major locus of selection on maternal and offspring behavior, physiology, immunology, and metabolism (Brown et al. 2013). Fetal, infant, and maternal mortality directly account for nearly one third of all mortality in both historically documented and contemporary nonindustrial societies (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 who successfully avoided the high mortality risks associated with pregnancy (mortality from genetic/chromosomal anomalies

notwithstanding), to have strategies to reduce mortality risks during their own pregnancies (Fessler 2002; Patil 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 stresses. Aversions to animal foods, chemically toxic plant foods, and highly glycemic plant foods among the women of Yasawa Island 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 essential micronutrients likely reflect motivational mechanisms that drive mothers to prioritize seeking out foods that reduce stress and promote tissue maintenance and generation.

This study, taken together with previous work, also indicates separate but related roles for physiological appetite changes during pregnancy and for culture in pregnancy-related diet changes. Although this paper focused on visceral aversions and cravings, a previous study by Henrich and Henrich (2010) shows that Yasawa Islanders have developed cultural prohibitions that discourage pregnant and lactating women from ingesting marine foods 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. 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 and 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 individual variation in nutritional status, especially variation in micronutrient sufficiency. If this proposal is correct, aversions may reflect a genetically based predisposition of women to motivate avoidances of 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 Holland and O'Brien's (2003) suggestion 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 individual variation in health parameters, from eating especially dangerous foods (but see Placek and Hagen 2015, for a case in which cultural proscriptions appear nonadaptive or perhaps maladaptive). Thus, aversions and taboos may have evolved in parallel via different systems of inheritance (one genetic and one cultural) to solve related but nonetheless distinct classes of ecological challenges faced during pregnancy.

With respect to future research, a priority should be to address the main shortcomings of the present study and of similar studies that have come before this one. Specifically, although 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 and fully evaluate the adaptive hypotheses. In particular, this study and other studies on pregnancy-related aversions and cravings lack pregnancy-by-pregnancy information on maternal nutritional status, adiposity, diet, or serum concentrations of appetite-regulating hormones such as ghrelin and leptin. Data of this type are necessary to formally and rigorously test the hypotheses in question. 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. We also lack data on elapsed time between last pregnancy and interview, which means that we cannot assess the extent to which variation in recall biases may have influenced our findings.

With the foregoing in mind, future studies should directly and prospectively test whether women (*a*) preferentially experience cravings for starches or other energy-dense foods when they are calorie-stressed, (*b*) preferentially experience cravings for animal foods when they are micronutrient stressed, or (*c*) preferentially experience cravings for fruits and vegetables when other nutritional priorities have already been met and accruing additional stores of vitamins, minerals, and fiber found in fruits and vegetables may enhance current and/or future reproductive status or generally make pregnancy more comfortable. 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.

Another useful undertaking would be to investigate the relationship between food aversions and taboos in pregnancy further, paying particular attention to individual variations likely to promote or repress expression of aversions. In a similar vein, we recommend the exploration of 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 during her first few months of pregnancy 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 are tantalizing. They 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 industrial

and small-scale populations concerning the factors that influence the development of these socially learned dietary recommendations and how such cultural factors interact with physiological craving sensations.

To conclude, the results of this study, when combined with those of McKerracher et al. (2015) and Henrich and Henrich (2010), suggest that the women of Yasawa cope with the substantial challenges posed by pregnancy through both genetic and cultural adaptations. This highlights the usefulness of studying human physiological and behavioral phenomena within the dual inheritance framework (Richerson and Boyd 2005).

Acknowledgments We gratefully acknowledge that financial support for this research was provided by Simon Fraser University (SFU), the University of British Columbia, the Social Sciences and Humanities Research Council of Canada, the Canada Foundation for Innovation, and the Canada Research Chairs program. Additionally, we are thankful to the Fijian research assistants whose diligent and meticulous fieldwork made this study possible. We also thank the members of SFU's Human Evolutionary Studies Program, SFU's FAB* lab, Aarhus University's Centre for Biocultural History, and four anonymous reviewers for thoughtful comments during the development of this manuscript. Lastly, we would like to express our deepest gratitude to the women of Yasawa Island for their willingness to share information about their personal histories. Without their assistance, this project and several others would have been impossible.

References

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.

Bath, S. C., Steer, C. D., Golding, J., Emmet, P., & Rayman, M. P. (2013). Effect of inadequate iodine status on UK pregnant women on cognitive outcomes in their children: results from the Avon Longitudinal Study of Parents and Children (ALSPAC). *The Lancet, 382*, 331–338.

Biesalski, H. K. (2005). Meat as a component of a healthy diet – are there any risks or benefits if meat is avoided in the diet? *Meat Science, 70*, 509–524.

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

Bonham, M. P., Duffy, E. M., Robson, P. J., Wallace, J. M., Myers, G. J., Davidson, P. W., et al. (2008). Contributions of fish to micronutrient intakes important for fetal development: a dietary survey of pregnant women in the Republic of Seychelles. *Public Health Nutrition, 12*, 1312–1320.

Bradbury, E. J., Duputie, A., Deletre, M., Roullier, C., Narvaez-Trujillo, A., Manu-Aduening, J. A., et al. (2013). Geographic differences in patterns of genetic variation among bitter and sweet manioc (*Manihot esculenta* subsp. *esculenta*; Euphorbiacea). *American Journal of Botany, 100*, 857–866.

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, 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.

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.

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

Crespi, B. J. (2011). The strategies of genes: Genomic conflicts, attachment theory, and the development of the social brain. In A. Petronis & J. Mill (Eds.), *Brain, behavior, and epigenetics* (pp. 143–167). Berlin: Springer.

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

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. (2006). 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). Paleolithic 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. (2002). Reproductive immunosuppression and diet: an evolutionary perspective on pregnancy sickness and meat consumption. *Current Anthropology, 43*, 19–61.

Fessler, D. M. T., & Navarrete, C. D. (2003). Meat is good to taboo: dietary proscriptions as a product of the interaction 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. (2000). Morning sickness: a mechanism for protecting mother and embryo. *Quarterly Review of Biology, 75*, 113–148.

Flaxman, S. M., & Sherman, P. W. (2008). Morning sickness: adaptive cause or nonadaptive consequence of embryo viability? *American Naturalist, 172*, 54–62.

Forbes, S. (2014). Pregnancy sickness and parent-offspring conflict over thyroid function. *Journal of Theoretical Biology, 355*, 61–67.

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 and 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. In S. C. Stearns & J. C. Koella (Eds.), *Evolution in health and disease* (pp. 77–90). Oxford: Oxford University Press.

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 revolution. *Current Anthropology, 44*, 707–711.

Hook, E. B. (1978). Dietary cravings and aversions during pregnancy. *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.

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.

Langley-Evans, S. C., & McMullen, S. (2010). Developmental origins of adult disease. *Medical Principles and Practice, 19*, 87–98.

Lee, J.-I., Lee, J.-L., & Lim, H.-S. (2004). Morning sickness reduces dietary diversity, nutrient intakes, and infant outcome of pregnant women. *Nutrition Research, 24*, 531–540.

Lozano, R., Naghavi, M., Foreman, K., Lim, S., Shibuya, K., Aboyans, V., et al. (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.

Maconochie, N., Doyle, P., Prior, S., & Simmons, R. (2007). Risk factors for first trimester miscarriage – results from a UK-population-based case-control study. *Epidemiology, 114*, 170–186.

McKerracher, L., Collard, M., & Henrich, J. (2015). The expression and adaptive significance of pregnancy-related nausea, vomiting, and aversions on Yasawa Island, Fiji. *Evolution and Human Behavior, 36*, 95–102.

Myatt, L. (2006). Placental adaptive responses and fetal programming. *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*, 3938–3942.

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.

Patil, C. L., & Young, S. L. (2012). Biocultural considerations of food cravings and aversions: an introduction. *Ecology of Food and Nutrition, 51*, 365–373.

Patil, C. L., Abrams, E. T., Steinmetz, A. R., & Young, S. L. (2012). Appetite sensations and nausea and vomiting in pregnancy: An overview of the explanations. *Ecology of Food and Nutrition*, *51*, 394–417.

Patti, M. (2013). Intergenerational programming of metabolic disease: evidence from human populations and experimental animal models. *Cellular and Molecular Life Sciences, 70*, 1–12.

Pearn, J., Harvey, P., De Ambrosis, W., Lewis, R., & McKay, R. (1982). Ciguatera and pregnancy. *Medical Journal of Australia, 1*, 57–58.

Pike, I. L. (2000). The nutritional consequences of pregnancy sickness: a critique of a hypothesis. *Human Nature, 11*, 207–232.

Placek, C. D., & Hagen, E. H. (2015). Fetal protection: the roles of social learning and innate food aversions in South India. *Human Nature*, *26*, 255–276.

Profet, M. (1988). The evolution of pregnancy sickness as protection to the embryo against Pleistocene teratogens. *Evolutionary Theory, 8*, 177–190.

Profet, M. (1992). Pregnancy sickness as adaptation: A deterrent to maternal ingestion of teratogens. In J. H. Barkow, L. E. Cosmides, & J. E. Tooby (Eds.), *The adapted mind* (pp. 327–366). New York: Oxford University Press.

R Development Core Team. (2008). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org.

Richerson, P., & Boyd, R. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.

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.

Sclafani, A. (1997). Learned controls of ingestive behaviour. *Appetite, 29*, 153–158.

Ségurel, L., Austerlitz, F., Toupance, B., Gautier, M., Kelley, J. L., Pasquet, P., et al. (2013). Positive selection for protective variants for type 2 diabetes from the Neolithic onward: a case study in Central Asia. *European Journal of Human Genetics, 21*, 1146–1151.

Sherman, P. W., & Flaxman, S. M. (2001). Protecting ourselves from food. *American Scientist, 89*, 142–151.

Sherman, P. W., & Flaxman, S. M. (2002). Nausea and vomiting of pregnancy in an evolutionary perspective. *American Journal of Obstetrics and Gynecology, 186*, 190–197.

Sherman, P. W., & Hash, G. A. (2001). Why vegetable recipes are not very spicy. *Evolution and Human Behavior, 22*, 147–163.

Steinmetz, A. R., Abrams, E. T., & Young, S. L. (2012). Patterns of nausea, vomiting, aversions, and cravings during pregnancy on Pemba Island, Zanzibar, Tanzania. *Ecology of Food and Nutrition, 51*, 418–430.

Svensson-Arvelund, J., Ernerudh, J., Buse, E., Cline, J. M., Haeger, J., Dixon, D., et al. (2013). The placenta in toxicology, part II: systemic and local immune adaptations in pregnancy. *Toxicologic Pathology, 42*, 327–339.

Thaman, R. R. (1990). Evolution of the Fiji food system. In A. A. J. Jansen, S. Parkinson, & A. F. S. Robertson (Eds.), *Food and nutrition in Fiji* (pp. 23–107). Suva: Institute of Pacific Studies.

Tierson, F. D., Olsen, C. L., & Hook, E. B. (1985). Influence of cravings and aversions on diet in pregnancy. *Ecology of Food and Nutrition, 17*, 117–129.

Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist, 14*, 249–264.

Weigel, M. M., Coe, K., Castro, N. P., Caiza, E., Tello, N., & Reyes, M. (2011). Food aversions and cravings during early pregnancy: association with nausea and vomiting. *Ecology of Food and Nutrition, 50*, 197–214.

Wells, J. (2009). Thrift: a guide to thrifty genes, thrifty phenotypes and thrifty norms. *International Journal of Obesity, 33*, 1331–1338.

Williams, G. C., & Nesse, R. M. (1991). The dawn of Darwinian medicine. *Quarterly Review of Biology, 66*, 1–22.

Wood-Bradley, R. J., Henry, S. L., Vrselja, A., Newman, V., & Armitage, J. A. (2013). Maternal dietary intake during pregnancy has longstanding consequences for the health of her offspring. *Canadian Journal of Physiology and Pharmacology, 91*, 412–420.

Young, A. G., & Pike, I. L. (2012). A biocultural framework for examining maternal cravings and aversions among pastoral women in East Africa. *Ecology of Food and Nutrition, 51*, 444–462.

Luseadra McKerracher is a PhD candidate and fellow in the Human Evolutionary Studies Program at Simon Fraser University (SFU) in Canada as well as a visiting researcher at the Centre for Biocultural History at Aarhus University in Denmark. Her research focuses on the evolutionary ecology of human life history and demography, with a particular focus on ecological influences on pregnancy and breastfeeding.

Dr. Mark Collard is the Canada Research Chair in Human Evolutionary Studies and a professor of archaeology at SFU. He also holds a personal chair in archaeology at the University of Aberdeen in the UK. In addition, he is the director of SFU's Human Evolutionary Studies Program (http://hesp.irmacs.sfu.ca/) and a co-director of the Centre for Human Evolution, Culture and Cognition, a research hub in Vancouver dedicated to the evolutionary study of human cognition and behaviour (http://www.hecc.ubc.ca/). Dr. Collard has published on a wide range of topics in archaeology and biological anthropology, including the determinants of gestation length and breastfeeding duration in primates and other mammals (http://profmarkcollard.com/publications/).

Dr. Joseph Henrich is a professor of human evolutionary biology at Harvard University and holds the Canada Research Chair in Culture, Cognition and Coevolution at the University of British Columbia, where he's also a professor in both economics and psychology. In 2009, he won the Early Career Award for Distinguished Scientific Contributions bestowed by the Human Behavior and Evolution Society. His latest book is *The Secret of Our Success*: *How Culture Is Driving Human Evolution*, *Domesticating Our Species*, *and Making Us Smarter* (Princeton University Press, 2016).