



Original Article

The expression and adaptive significance of pregnancy-related nausea, vomiting, and aversions on Yasawa Island, Fiji[☆]

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ABSTRACT

We report a study on nausea and vomiting of pregnancy (NVP) and pregnancy-related food aversions in a small-scale society from Yasawa Island, Fiji. Because NVP has rarely been studied quantitatively in small-scale populations, we begin with a detailed description of its expression among the women of Yasawa. We found that 66% of these women experience nausea and/or vomiting in tandem with the development of aversions to certain foods. This pattern of expression is similar to what has been documented for industrialized populations, and the prevalence of 66% is close to the industrialized mean prevalence of 69%. We then use the data from the women of Yasawa to evaluate the three main hypotheses that have been put forward to explain the evolution and ecological function of NVP. We show that food aversions of pregnancy focus preferentially on food types that are more likely to carry pathogens or contain chemical toxins. Such aversions do not focus on nutrient-dense foods or on frequently encountered foods. These findings are most consistent with the hypothesis that NVP, along with pregnancy-related aversions, evolved to motivate women to avoid exposure to diseases and other toxins when they are immune-compromised by pregnancy and during a critical period of embryo development. These findings contribute to a growing body of theoretical and empirical literature that suggests that NVP symptoms represent a series of adaptations rather than pathological responses to the physiological demands of pregnancy.

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1. Introduction

Sometimes called “morning sickness” or “pregnancy sickness”, Nausea and Vomiting of Pregnancy (NVP) refers to a suite of symptoms that many women experience to varying degrees and in varying combinations during early pregnancy. These symptoms include nausea, gagging, retching, vomiting, dizziness, and fatigue (Firoz, Maltepe, & Einarson, 2010). Increased olfactory sensitivity (Nordin, Broman, Bringlov, & Wulff, 2007; Nordin, Broman, & Wulff, 2005) and the development of novel aversions to specific foods, social situations, and/or sexual behaviors (Fessler, Eng, & Navarrete, 2005; Navarrete, Fessler, & Eng, 2007; Young & Pike, 2012) generally accompany NVP and appear to relate to it both temporally and functionally (Patil, Abrams, Steinmetz, & Young, 2012).

Currently, NVP is thought to affect approximately 60% of women during at least one of their pregnancies (Flaxman & Sherman, 2000). However, this prevalence estimate is based largely on Western populations (Patil et al., 2012) and therefore may be inaccurate. Western food production and health care systems differ substantially from those in many other places, and these factors may influence NVP expression. Significantly, the limited evidence from populations from a more diverse range of countries suggests that NVP prevalence varies cross-culturally (Einarson, Piwko, & Koren, 2013; Pepper & Roberts, 2006) and that some non-Western populations have lower rates than have been documented for Western nations (e.g. Anath & Rath, 1993; Christian et al., 1998).

NVP is puzzling from an evolutionary perspective (Fessler, 2002b; Flaxman & Sherman, 2000) because the expression of the appetite-suppressing features of NVP in early pregnancy (e.g. nausea, vomiting, and food aversion) limits maternal and fetal access to energy and other nutrients that promote fetal growth (e.g. Latva-Pukkila, Isolauri, & Laitinen, 2010; Lee, Lee, & Lim, 2004). Despite these costs, however, such symptoms are associated with reduced risk of spontaneous abortion (Forbes, 2002; Huxley, 2000), and increases in NVP severity correlate with improved outcomes in other measures of fetal survivorship and in infant and young child health (e.g. Latva-Pukkila et al., 2010; Nulman et al., 2009; Weigel & Weigel, 1989). This counter-intuitive pattern raises two important questions. First, is NVP a feature of most healthy, non-abortive human pregnancies regardless of ecological context or is it an

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anomaly of industrial socioeconomic systems? Second, if NVP affects most populations, why might it have a positive rather than a negative impact on pregnancy outcome?

Here, we report a study designed to address these questions. The study focused on an indigenous population of small-scale fisher-farmers from Yasawa Island, Fiji. In the first section of the study, we used recall-based interview data from women of Yasawa Island to generate summary statistics regarding the expression of NVP and related symptoms in this population, and then compared these statistics to those documented for other populations. In the second part of the study, we used the interview data to test the three main hypotheses that have been proposed to explain why NVP might have evolved despite its costs. The study, which is among the first to systematically assess NVP in a small-scale society, supports the hypothesis that NVP is a feature of the majority of healthy human pregnancies, and suggests that it evolved to protect the developing fetus from exposure to pathogens and chemical toxins.

2. Data collection

The data were collected in 2005–2006 as part of an on-going project led by one of us (JH) on the lifeways, psychology, culture, and evolutionary ecology of a population indigenous to Yasawa Island, Fiji.

Yasawa, situated on the northwestern edge of the Fijian archipelago, has a seasonal climate, featuring a hot, wet season, and a relatively mild, dry season. The island is home to ~900 people who live in six villages. The majority of Yasawans are subsistence-level fisher-horticulturalists (Henrich & Broesch, 2011; Henrich & Henrich, 2010). Subsistence is based heavily on cultivated root vegetables (primarily cassava and yams), cultivated fruits (primarily coconuts and bananas), gathered shellfish and other littoral resources, fish, and some imported processed foods (primarily tea, sugar, and wheat flour). Men maintain garden plots and fish, while women gather wood and littoral resources, prepare food, provide childcare, and carry out most other household tasks. Children assist with gathering and childcare. Additional information regarding the study site and the participants is provided in the supplementary materials (S Text 1).

Trained female Fijian field assistants interviewed 70 mothers from randomly sampled households in three Yasawan villages about nausea, vomiting, and related sensations, a phenomenon called “*kuna ca*” in Standard Fijian. Specifically, mothers were asked whether they had experienced *kune ca* during their most recent full term pregnancies and, if so, during what months they had experienced it. They were also asked to freely list any symptoms of pregnancy they could recall. Subsequently, they were asked if they experienced any of the following: nausea, vomiting, headache, dizziness, loss of appetite, or diarrhea. Women were also asked about food aversions during the interview. The interviewers asked women to freelist any items they normally like but found aversive during pregnancy. Then, women were asked if any of the following foods became aversive during pregnancy: shellfish, fish, meat, vegetables, fruit, dairy products, sweets, spices, cassava, yams, turtle, moray eel, octopus or squid, porcupine fish, freshwater eel, barracuda, and shark. Additionally, because in pilot interviews women had spontaneously reported novel aversions to their husbands, each interviewee was asked if the smell of her husband bothered her during her pregnancy.

Twenty randomly selected female heads of households were also interviewed about the composition of their households’ diets.

All interviews were carried out in standard Fijian and subsequently translated to English before coding and analyses.

3. Part I: expression of NVP on Yasawa, and comparison to global sample

The first part of this study had two aims. The first was to diagnose and characterize NVP and related symptoms among the women of

Yasawa Island. The second was to compare the proportion of women from Yasawa that experience NVP to NVP prevalence in other populations from around the globe.

We describe expression of NVP on Yasawa in detail because, although ethnographers have previously reported anecdotes of pregnant women in small-scale societies experiencing nausea and vomiting, these reports do not tell us how frequently the phenomenon occurs in such populations (Flaxman & Sherman, 2000; Minturn & Weiher, 1984). To our knowledge, only one previous study, carried out by Pike (2000) on Turkana pastoralists of Kenya, has investigated prevalence of NVP in a small-scale society. So, our study provides one of only two pieces of quantitative evidence that NVP is a common feature of pregnancy in subsistence-level populations.

We used both the freelist data and the checklist data regarding NVP symptoms to retrospectively diagnose women with NVP following the differential diagnosis guidelines outlined for Western clinical populations by Firoz et al. (2010), independent of whether the women self-diagnosed with *kune ca*.

Our main findings regarding the rates at which the women of Yasawa Island experience NVP-related symptoms are summarized in Table 1. We found that, of the 70 women interviewed, 47 (67%) reported having experienced *kune ca* in their most recent pregnancies. Of these, we diagnosed 46 (66% of the sample) with NVP, according to Firoz et al.’s (2010) guidelines. None of the women who reported not experiencing *kune ca* had clinical NVP symptoms. All 46 (100%) women with NVP reported having vomited at least once and 44 (96%) of them reported having felt nauseous. Many of these same women also reported other uncomfortable symptoms during their pregnancies, including loss of appetite (98% of those with NVP), headaches (85%), and/or diarrhea (15%).

Regarding the timing of NVP, 19 (41%) of the 46 women with NVP reported that they experienced nausea and vomiting exclusively in the first trimester of their pregnancies, 31 (67%) during the first four months, and 42 (93%) during the first two trimesters.

All of the women with nausea and vomiting developed at least one novel food aversion during their pregnancies. We also found that 19 (41%) of the 46 Yasawan women with NVP became averse to the smell of their husbands during their pregnancies.

Thus, the data strongly suggest that NVP exists on Yasawa. The expression of *kune ca* on Yasawa is consistent with how NVP has been described for other populations. That is, nausea and vomiting often occur with one another and with some combination of headaches, fatigue, dizziness, and the development of novel aversions, primarily during the first three to four months of pregnancy (Firoz et al., 2010; Flaxman & Sherman, 2000; Patil et al., 2012). Our main unexpected finding was that many Yasawan women were strongly averse to the smell of their husbands during pregnancy; this phenomenon has only been documented anecdotally previously (see Steinmetz, Abrams, & Young, 2012: p. 424).

Table 1

Summary statistics for *kune ca* prevalence, and specific NVP symptoms including nausea, vomiting, headache, dizziness, fatigue, food aversions, husband aversions among the women of Yasawa Island.

Symptoms (S) and Correlates (R) of NVP	Number of women in sample with symptom	% of women in sample with symptom
Nausea (S)	44	63%
Vomiting (S)	46	66%
Headache and/or dizziness (S)	34	47%
Diarrhea (R)	7	10%
Loss of Appetite (R)	45	64%
Food Aversions (R)	68	97%
Aversions to smell of husband (R)	19	41%
Report <i>Kune ca</i>	47	67%

Regarding the second objective for this section of the study – comparison of the prevalence of NVP on Yasawa to global NVP prevalence rates for previously studied populations – we used the diagnosed rate of 66% as the Yasawan rate. We then took published prevalence rates for comparator populations from a cross-national study by [Pepper and Roberts \(2006\)](#). The sample contained ten outliers, six of which we excluded either because they reflected values based solely on vomiting prevalence rather than total NVP prevalence or because they focused on a distinct subset of a population (e.g. adolescent mothers or mothers with eating disorders). The other four outliers appeared reliable, so we retained them. Because the culled dataset contained only 10 populations from non-Western countries, we supplemented it with NVP prevalence data from what we believe to be the only five additional studies on non-Western populations that have been published in English between 2006 when the Pepper and Roberts study went to press and August 2013 when we completed our review of the relevant literature. These studies include one carried out in Turkey ([Nazik & Eryilmaz, 2014](#)), two from Tanzania ([Nyaruhucha, 2009](#); [Steinmetz et al., 2012](#)), and two from Ecuador ([Weigel et al., 2011, 2006](#)). The combined dataset comprises values for 55 study populations from 22 countries. These data were used to generate descriptive statistics regarding global variation in NVP prevalence. These and all subsequent analyses were carried out in R ([R Development Core Team, 2008](#)), with the exception of [Fig. 2](#) in the second part of the study, which was made using SPSS 17.0.

We summarize cross-national variation in NVP prevalence in [Fig. 1](#). We found that Yasawa's NVP prevalence rate is not unusual in global perspective. In our updated version of the global dataset, NVP prevalence ranges from 35% in one sample from India to 90% in two samples, one from the United Kingdom and one from Korea. Mean NVP prevalence for this full sample is $69\% \pm 1.7$, with a median of 69%, and mode of 67%. The range of variation among the 15 non-Western countries (35%–90%) slightly exceeds that of the 39 Western countries (46%–90%), although the means of the two groups (respectively: $66\% \pm 4.5$ and $70\% \pm 1.6$) are statistically indistinguishable ($t = -0.761$, $p = 0.457$). The Yasawan prevalence of 66% falls near the central tendencies of all of these ranges. These findings suggest that NVP is expressed among Yasawa Islanders at a rate similar to those documented for larger scale populations.

Characterizing the expression and prevalence of NVP on Yasawa Island and comparing these to global data highlight the point that NVP exists at a non-trivial rate in a small-scale society with a predominantly local diet. This result, as with the previous Turkana study ([Pike, 2000](#)), suggests NVP is not a derived feature of large-scale, industrialized societies. Rather, NVP likely constitutes a feature of pregnancy that affects women in a wide variety of socioeconomic and ecological settings.

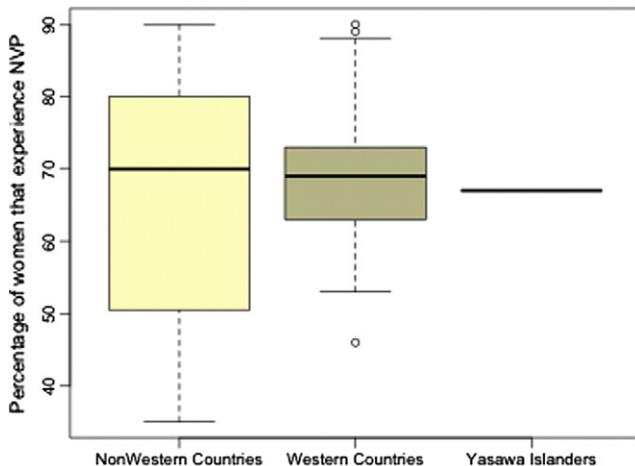


Fig. 1. Boxplots of cross-national variation in NVP prevalence. The prevalence of NVP among Yasawa Islanders of Fiji is shown to the right of prevalence rates from populations from Western and Non-Western countries.

Furthermore, prevalence of NVP on Yasawa falls near the central tendencies for the global sample, the Western sub-sample, and the non-Western sub-sample, perhaps hinting that there may be some tendency, across populations and across ecological circumstances, for about two-thirds of women to experience NVP.

4. Part II: testing evolutionary hypotheses for NVP using data from Yasawa Islanders

In the second part of our study, we used data from Yasawa Islanders regarding pregnancy-related aversions and non-pregnancy household diet to test a series of hypotheses regarding why NVP and related symptoms occur in contemporary populations.

4.1. Hypotheses

Four main explanations for NVP can be identified in the literature. Three of these explanations explicitly assume that NVP evolved either as a direct solution to an adaptive challenge or as a by-product of a solution to an adaptive challenge. The fourth explanation assumes that NVP symptoms represent pathologies rather than adaptations or by-products of selection.

The first of the evolutionary hypotheses for NVP is the “maternal-embryo protection hypothesis” or “MEPH” ([Fessler, 2002a, 2002b](#); [Flaxman & Sherman, 2000](#)). Two well-understood features of pregnancy physiology form the basis of this hypothesis:

- 1) Pathogens and teratogens can have particularly harmful, long-lasting impacts when exposure occurs during embryo tissue differentiation, during the first 12 weeks of pregnancy ([Langley-Evans, 2006](#); [Myatt, 2006](#); [Rillamas-Sun, 2010](#)).
- 2) Mothers down-regulate their immune functions during early pregnancy to facilitate the tolerance of embryo tissues, which maternal immune systems would otherwise recognize as “non-self” and attack ([Fessler, 2002b](#); [Svensson-Arvelund et al., 2014](#)). This maternal immune suppression enables tolerance of embryos but also leaves both mothers and embryos vulnerable to pathogens and chemical toxins.

The MEPH, then, holds that NVP is an adaptive solution to the problem of fetal and maternal vulnerability to pathogens and teratogens during early pregnancy ([Flaxman & Sherman, 2000, 2008](#); [Hook, 1978](#); [Profet, 1988](#)). The core assumption of this hypothesis is that mothers unconsciously compensate for their immunological vulnerability by developing novel aversions (via nausea) and/or by expelling potential sources of pathogens and teratogens (via vomiting).

The second evolutionary explanation for NVP is the “compensatory placental growth hypothesis” or “CPGH” ([Coad, Al-Rasasi, & Morgan, 2002](#); [Huxley, 2000](#)). This hypothesis suggests that mothers and embryos differ in their genetic interests in embryo health and survivorship, and that these differences drive struggles between mothers and embryos over limited maternal energetic resources. Mothers may sometimes improve their lifetime fitness by terminating a particular pregnancy early and redirecting energy towards a future pregnancy. Before complete placental invasion around gestation week 12, mothers may reject and spontaneously abort embryos relatively easily if the quality of an embryo is poor or if maternal resources are tightly circumscribed ([Forbes, 2002, 2014](#)). Embryo fitness, on the other hand, most often benefits if the embryo avoids abortion and procures as many resources from its mother as possible ([Haig, 1993](#); [Trivers, 1974](#)). So, embryos hormonally advertise their viability to reduce risk of abortion and to demand maternal resources. The CPGH holds that one way embryos may secure energy for placental development is to repress maternal appetite during early pregnancy by causing nausea and vomiting. This idea derives from evidence suggesting that, during early pregnancy, mildly calorie-restricted mothers prioritize allocating energy to current reproduction through increased placental growth ([Huxley, 2000](#); [Lunney, 1998](#); see also [Weigel et al., 2006](#)). Well-nourished mothers, in contrast,

often reserve energy for subsequent reproductive events instead of investing exclusively in an existing fetus. As such, according to the hypothesis, embryos trigger NVP in their mothers when calories and other nutrients are not otherwise restricted to favor investment in their own development.

The “by-product of genetic conflict” (hereafter, “by-product”) hypothesis resembles the CPGH in that they both hold that NVP results from a conflict between mother and embryo over maternal energetic resources. Additionally, both hypotheses assume that embryos have evolved to hormonally advertise their viability to their mothers. However, while the CPGH argues that NVP represents a hormonally mediated strategy to repress maternal appetite, the by-product hypothesis argues that these hormonal signals *inadvertently* (i.e. non-adaptively) cause disruptions to maternal endocrinology that trigger immune responses such as nausea or vomiting (Forbes, 2002, 2014).

As noted, the fourth approach to understanding NVP conceives of the symptoms as pathologies (Sherman & Flaxman, 2002). Although many proponents of this hypothesis acknowledge the puzzle of the observed negative correlation between NVP severity and risk of spontaneous abortion (e.g. Irving, 1940; Weigel & Weigel, 1989), few offer functional explanations for this phenomenon and instead focus on pharmacological interventions that reduce NVP symptoms (e.g. Anderka et al., 2011; Clark, Costantine, & Hankins, 2012; Tan & Omar, 2011). The pathology approach does not seek to explain NVP’s existence and therefore does not offer clear predictions about functional relationships among NVP symptoms or between NVP symptoms and ecology. However, from the view of natural selection theory, the approach does predict that NVP should be rare and should not be associated with improved pregnancy outcomes. Because the existing evidence clearly contradicts these predictions (Flaxman & Sherman, 2000; Sherman & Flaxman, 2002), we will not evaluate this hypothesis here.

4.2. Predictions

The three evolutionary hypotheses yield different predictions about what foods and other stimuli for nausea and/or vomiting are most likely to become aversive to women during early pregnancy (Steinmetz et al., 2012; Weigel et al., 2011). The MEPH, which frames NVP as a mechanism to compensate for maternal immuno-suppression, predicts that pregnant women should preferentially develop novel aversions to foods that are potentially high in pathogen load such as meat and fish and/or in teratogenic chemical toxins, such as most plant foods with strong spicy or bitter flavors (Fessler, 2002b; Flaxman & Sherman, 2000, 2008; Patil et al., 2012). The MEPH also predicts that women may develop aversions to other potential sources of pathogens and teratogens, such as body fluids, nonhuman animals, and even strangers (Fessler et al., 2005; Navarrete et al., 2007). Under the CPGH, which contends that NVP serves to prevent mothers from consuming nutrient-dense foods, we expect maternal food aversions to focus particularly on high-quality foods that lend themselves to maternal fat gain (Steinmetz et al., 2012). The by-product hypothesis, which holds that hormonal disturbances due to genetic conflict trigger nausea and vomiting, suggests that women will experience nausea regardless of external triggers. Because evidence indicates that nausea experienced during exposure to a food often results in the acquisition of a new food aversion (Pelchat & Rozin, 1982), this hypothesis predicts that whatever foods are most frequently encountered by a woman are most likely to be accidentally associated with a conflict-related episode of nausea and thus most likely to become aversive.

4.3. Evaluations of hypotheses for NVP using data from Yasawa Island

We used data from Yasawa Islanders regarding pregnancy-related aversions and non-pregnancy household diet to test the above predictions of the evolutionary hypotheses for NVP and related symptoms. The food aversions data were taken from the same 70

interviews used in the section on expression of NVP. The diet data were taken from interviews with 20 randomly sampled female heads of households in which each woman was asked to recall all foods she had prepared for herself and her family the day prior to the interview and to report the quantity of each food prepared.

We employed multiple Ordinary Least Squares (OLS) regression analysis of the food aversions and diet data to evaluate the predictions of the three hypotheses. We also took into account the evidence that many of the interviewed women reported developing novel aversions to the smell of their husbands during early pregnancy. The hypotheses and their test predictions are summarized in Table 2.

The outcome variable in the regression represents a count of Yasawa women that reported a novel, pregnancy-related aversion to a particular food category. To create this variable, we coded the freely listed items and the targeted items regarding food aversions, and then binned the data into eleven categories. These categories include, alphabetically: cassava; dairy; fish; fruit; imported starches and sweets (labeled “imported starches”); locally grown-starches other than cassava (“local starches”); marine resources other than fish (“non-fish marine”); meat; mild-tasting vegetables; oils and fats; and spicy/sour/bitter vegetables. Then, we tallied the number of women that reported an aversion to each category. We provide further details on category selection and on how we combined the freelist and checklist data in the supplement (S Text 2.1).

To create the first independent variable, we assigned each food category a pathogenicity–teratogenicity score – designed to measure both separate and combined effects of pathogens and chemical toxins in each food category – between one and 13. Initial scores concerned pathogenicity only, and ranged between one and seven. These pathogen scores were rankings based on the number of cases of food-borne illness attributed to a particular food category in the US between 1998 and 2008 by the national Center for Disease Control (Gould et al., 2013), adjusted for US food category consumption biases (using US 2006 data, FAOSTAT, 2013). To generate our overall measure of pathogenicity–teratogenicity, we added seven additional points to the pathogen riskiness scores of each of the food categories known to *frequently* contain chemical toxins (cassava and fish); 3.5 points to each of the food categories thought to *sometimes* contain chemical toxins (non-fish marine foods and spicy/sour/bitter plant foods); zero points were added to the remaining categories, thought not to contain teratogens. Details on the data sources and how we calculated these scores are available in S Text 2.2.

The second independent variable is the macronutrient density of each food category, derived from the household diet data. To estimate the proportion of macronutrients that each food category contributes to the diet of Yasawa Islanders, we converted food quantity estimates that the women had reported in volumes into (1) daily caloric yield, (2) daily grams of protein, and (3) daily grams of fat. We did so using the US Department of Agriculture’s Nutrient Database for Standard Reference (2012), which provides nutrient profiles for a wide variety of foods. In cases in which a Fijian food type was not represented in the

Table 2

Hypotheses for the evolution of NVP and their predictions regarding foci for novel aversions during pregnancy.

Hypothesis	Test Predictions
Maternal-embryo protection	<ul style="list-style-type: none"> Number of women that develop novel aversions to a particular food category correlates positively with the pathogenicity–teratogenicity of that category Women may develop aversions to other key non-food sources of pathogens or teratogens
Compensatory placental growth	<ul style="list-style-type: none"> Number of women that develop novel aversions to a particular food category correlates positively with the macronutrient density of that category
By-product of genetic conflict	<ul style="list-style-type: none"> Number of women that develop novel aversions to a particular food category correlates positively with frequency with which women encounter that category (encounter frequency)

database, we substituted similar foods that were represented. After characterizing the nutrient content of each food type, we binned these data into the same eleven categories that we used for the aversions data. We then estimated how much each food category contributes to the Yasawan diet by dividing the amount of macronutrients from each food category from all 20 households surveyed by the total number of macronutrients consumed in a day for all households. Next, we used Principal Components Analysis (PCA) to reduce the three dimensions of macronutrient content into a single proxy variable accounting for 40.4% of the among-category variation in macronutrient yield and saved the score of the first component as a variable. See S Text 2.3 for more information on the calculation of the macronutrient densities of each food category and on the PC loadings (S Text 2.3)

The last independent variable, “encounter frequency”, uses the household diet data to proxy how often women encounter each food category. Specifically, we counted the number of times women reported having prepared foods from each of the food categories. The raw encounter frequency data are available in the supplement (S Text 2.4).

The results of the OLS regression analysis are summarized in Table 3 and in the added variable plots presented in Fig. 2A–C. We found that the model accounts for ~64% of the variation in food category aversiveness. Pathogenicity–teratogenicity score is the only significant predictor in the model, with a beta coefficient of 0.69. Number of women that develop novel aversions to a particular food category was not significantly related to that category’s macronutrient density or to how frequently women encounter it when pathogenicity–teratogenicity was controlled.

In addition to our main analyses presented here, we carried out two sets of supplemental analyses, reported in S Text 3. In the first, we assessed the robusticity of our results to alternative scorings of pathogen–teratogen risk, with teratogenicity weighted $1\frac{1}{2}$, $\frac{1}{2}$, and $2/7$ as heavily as pathogenicity. We did this because we lack clear theoretical or empirical guidelines as to whether chemical toxicity poses a greater, equal, or lesser threat to mothers and embryos than pathogenicity. All scorings produced similar results regarding evaluations of the hypotheses, except for the case in which teratogenicity was weighted only $2/7$ as heavily as pathogenicity. In this last case, we could not reject the null hypothesis that the predictors have no impact on category aversiveness (S Text 3.1). In the second set of supplementary analyses, we modeled our error assuming a negative binomial (NB) distribution rather than a normal one because the number of pregnancy-related food category aversions among the women of Yasawa Island is count data with a mean distant from zero. Such data often have approximately normal error compatible with easily-interpretable OLS models; however, the NB distribution may provide a better approximation of the error. We found that, in regressions assuming an NB distribution, pathogenicity and teratogenicity risk score was the only predictor yielding a slope clearly distinguishable from zero (S Text 3.2).

So, overall, the regression results suggest the MEPH provides the best explanation for variation in number of women that develop novel aversions to a particular food category, at least in this population.

Furthermore, as mentioned previously, 19 of the women in the Yasawan sample reported novel aversions to the smell of their husbands. Fessler et al. (2005) predicted this finding, and it is consistent with the MEPH. Other people constitute sources of contagion, and

sexual or romantic partners may expose one another to pathogens through a particularly wide range of transmission mechanisms (Schaller & Murray, 2008). So, if women are experiencing NVP to protect themselves and their embryos during first trimester immunosuppression, it is likely that they would be motivated to avoid a variety of pathogen threats, including those potentially carried by their husbands and transmitted sexually. Notably, neither the by-product hypothesis nor the CPGH provides a logically sound explanation for why women may be averse to their husbands’ smell during early pregnancy.

Taken together, then, the data from Yasawa Island support the MEPH. They do not support the CPGH or the by-product hypothesis.

5. Discussion and conclusions

In the first part of our study, we found that NVP characterizes the pregnancies of the majority of Yasawan women, and that both the expression and prevalence of NVP among Yasawan women are comparable to what has been documented for large-scale, industrial populations. Unexpectedly, we also found that, during pregnancy, many Yasawan women develop aversions to the smell of their husbands. In the second part, using Yasawa Islander data to test three evolutionary hypotheses for NVP, we found that Yasawan women are most likely to develop pregnancy-related aversions to foods high in pathogens such as meat, fish, and shellfish as well as to foods high in chemical toxins such as cassava. These results reported in the second section are consistent with the predictions of only one of the three hypotheses, the maternal-embryo protection hypothesis (MEPH).

There are at least two reasons to be cautious of the findings of the second portion of our study, however. First, because comprehensive food-borne illness surveillance and food composition data were not available for Pacific Island foodstuffs, we used US-based data to estimate both the pathogenicity and nutrient composition of each of the food categories represented in our dataset. We suspect that the US-based illness data likely underestimate the pathogenicity of Yasawan animal foods (because animal foods are generally refrigerated in the US but not on Yasawa) and overestimate the pathogenicity of fruits and vegetables (because plant foods are often stored for long periods of time and widely distributed in the US but not on Yasawa). If this supposition is correct, the US-based pathogenicity score used in this study may provide a relatively conservative test of the predictions of the MEPH. But, we cannot assess this assumption until future research evaluates the epidemiology of food-borne illness on Yasawa Island. Similarly, future research should also test our assumption that the relative nutrient density of Yasawan foods varies among food categories in a pattern similar to those of matched US foods.

The second reason to treat the findings cautiously is that we lack an established system for comparing teratogenicity among food categories and for integrating that system with a pathogenicity scoring system. So, we used a very coarse teratogenicity metric and weighted it equally with pathogenicity, then explored the consequences of altering this weighting system. Our findings suggest that our results, while consistent among three different weightings, do not stand up in a fourth condition in which teratogenicity is weighted only $2/7$ as heavily as pathogenicity. As such, our results are best interpreted as consistent with the predictions of the MEPH, with the caveat that this

Table 3

Results from OLS regression of number of women with aversions to a particular food category on possible predictors of that food category’s aversiveness.

Predictor	β	Estimate	Lower bound for bootstrapped 95% confidence interval	Upper bound for bootstrapped 95% confidence interval	p
Pathogenicity–teratogenicity risk score of food category	0.688	2.951	2.340	3.526	0.034
Score of food category’s contribution to macronutrient composition of normal household (non-pregnancy) diet on Yasawa Island (Macronutrient density)	0.224	3.715	1.547	6.847	0.457
Frequency at which women prepare foods from each food category on Yasawa Island (Encounter frequency)	0.110	0.099	-0.065	0.180	0.634

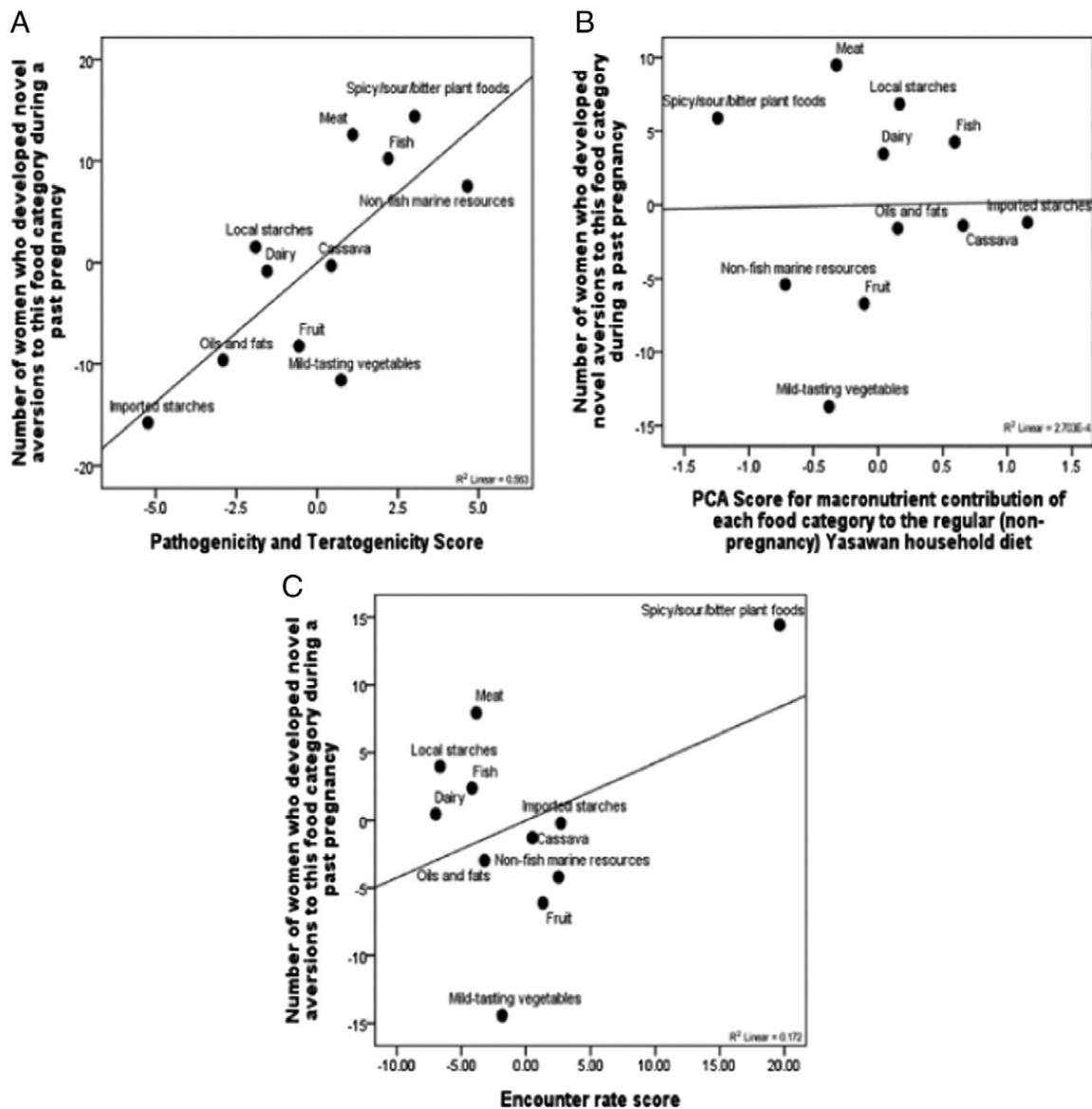


Fig. 2. Relationships between rates at which women develop novel aversions to food categories and characteristics of those food categories. (A) Added variable plot of rate of food category's aversiveness and its pathogenicity–teratogenicity risk score. (B) Added variable plot of rate of a food category's aversiveness and its score for the extent to which it contributes to the macronutrient density of regular household (non-pregnancy) diet on Yasawa Island. (C) Added variable plot of rate of food category's aversiveness and the frequency with which women from Yasawa Island encounter foods from that category.

interpretation only holds if chemical toxins are at least half as likely to present threats to fetal development as pathogens.

Despite these limitations, our study has theoretical and practical implications, and indicates several routes for future research. With respect to the description of the expression of NVP and related symptoms on Yasawa, our study is the second to differentially diagnose NVP and quantify its prevalence in a small-scale, subsistence-level population, pre-dated only by one study on NVP in marginally-nourished Turkana pastoralists in Kenya (Pike, 2000). Additionally, our study is one of only a few studies to formally describe and diagnose NVP outside of populations from Western countries. Studies in non-Western populations and especially in small-scale populations are necessary if we want to understand the extent to which NVP prevalence varies and to identify the factors that drive the variation in question (Patil et al., 2012). So, future work should seek to characterize NVP in other subsistence-level populations and compare the data to those yielded by the studies of Yasawa Island and Turkana women.

Lastly regarding the first section of our study, we found that women of Yasawa develop novel aversions to the smell of their husbands during

pregnancy. This phenomenon has not been systematically studied previously, although it has been reported anecdotally at least once before (Steinmetz et al., 2012: p. 424). Future research on Yasawa Island should investigate which factors influence whether a husband's smell is likely to become aversive to a pregnant woman. In particular, we would like to assess whether a husband's hygiene, social gregariousness, or sexual promiscuity increases his aversiveness. Additionally, future research on pregnant women in other populations should explore whether olfactory aversions to mates are common in other socioecological contexts and, if so, under what circumstances such aversions arise.

Our evaluation of the evolutionary hypotheses for NVP highlights two points. First, the finding that the data from the women of Yasawa Island are most consistent with the MEPH supports and clarifies the findings of several cross-national/cross-cultural studies as well as those of previous within-culture studies on variation in NVP expression. In particular, among-population analyses carried out by Fessler (2002a, 2002b), Flaxman and Sherman (2000), Minturn and Weiher (1984), and Pepper and Roberts (2006) indicate that food aversions of pregnancy focus preferentially on animal foods and that NVP prevalence is

higher in populations in which animal foods constitute a larger portion of the diet. Similarly, a series of within-population studies in Ecuador, Kenya, Tanzania and the US suggests that, during early pregnancy, women are relatively likely to develop aversions to meat and/or fish (Hook, 1978, 1980; Nyaruhucha, 2009; Olusanya & Ogundipe, 2009; Steinmetz et al., 2012; Weigel et al., 2011). Given that most animal foods are more likely to contain non-detectable biotoxins than most plant foods (Fessler, 2002a; Fessler & Navarrete, 2003), these within- and among- population patterns have generally been interpreted as support for the MEPH. However, animal foods constitute not only potential pathogen risks but also high quality, nutrient-dense foods (Sailer, Gaulin, Boster, & Kurland, 1985). The CPGH suggests that, in calorie-rich environments, embryos should manipulate their mothers to avoid such foods. So, many of the key findings regarding aversions to animal foods or correlations between NVP prevalence and contribution of animal foods to the diet can be interpreted as supporting both the CPGH and the MEPH.

In contrast, our study quantitatively evaluated whether aversions were most focused on foods high in pathogen and teratogen load or high in nutrient density, and found evidence that pathogenicity and teratogenicity are the strongest predictors of food category aversiveness. These results offer support for previous interpretations of evidence regarding aversions to animal foods that suggest that such foods are especially aversive to pregnant women because of their possible toxicity rather than their nutrient density. They also highlight the need for additional studies in other populations that take both the quality and the pathogenicity of animal foods into account when testing hypotheses for NVP.

Secondly, irrespective of the selective mechanism for the evolution of NVP, the evidence from Yasawa supports the view that NVP and its correlates represent a suite of evolved characters rather than pathological symptoms, further justifying rejection of the pathology hypothesis. That is, Yasawan women avoid foods and develop NVP in the patterns predicted by at least one of the evolutionary hypotheses and these patterns would be difficult to explain if NVP were pathological. Our finding that pregnancy-related food aversions on Yasawa are strongly patterned and non-pathological is in keeping with a growing corpus of data from a wide variety of other studies (see recent review by Patil et al., 2012). We suggest that viewing NVP as adaptive rather than pathological may require using different language than what has previously been used in clinical literature. In particular, describing NVP as a “syndrome” or a “set of symptoms” implies that it is a pathology. Future work that treats NVP as an adaptation should perhaps use the more neutral vocabulary of evolutionary biology and describe NVP as the expression of one or more behavioral and physiological traits.

Supplementary Materials

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.evolhumbehav.2014.09.005>.

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