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THE EXPRESSION AND ADAPTIVE SIGNIFICANCE OF PREGNANCY-RELATED NAUSEA, VOMITING, AND AVERSIONS ON YASAWA ISLAND, FIJI

Running headline: Nausea and Vomiting of Pregnancy in Fiji

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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, fatigue (Firoz et al., 2010), increased olfactory sensitivity (Nordin et al., 2005; 2007), and the development of novel aversions to specific foods, social situations, and/or sexual behaviours (Fessler et al., 2005; Navarrete et al., 2007; Young and Pike, 2012).

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

NVP is puzzling from an evolutionary perspective (Fessler, 2002; Flaxman and 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 et al., 2010; Lee et al., 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 and 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 anomaly of certain socioeconomic systems? Second, if so, why might NVP be expected to 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 rates at which NVP symptoms are expressed in this population, and to compare these rates to those documented for other populations. In the second part of the study, we used the interview data in a series of regression analyses to test the three main hypotheses that have been proposed to explain why NVP might have evolved despite its costs. The study, which may be 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 is an adaptation geared toward limiting the impact of pathogens and chemical toxins on the developing fetus.

DATA COLLECTION

The data were collected in 2005-2006 as part of an on-going project led by one of us on the lifeways, culture, and evolutionary ecology of Fijian population living on Yasawa Island. This project was approved by the University of British Columbia's Behavioral Research Ethics Board.

Yasawa is situated on the northwestern edge of the Fijian archipelago. The climate is warm and bi-seasonal, featuring a hot, wet season, and a relatively mild, dry season. Yasawa is home to approximately 900 people, who live in six villages. While a small percentage of people work in a resort and a few people hold vocational positions in health care, education, or the clergy, the majority of Yasawans are subsistence-level fisher-horticulturalists (Henrich and Broesch, 2011; Henrich and 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, water, and mollusks, prepare food, provide childcare, and carry out most other household tasks. Children assist with gathering and with childcare.

Under our supervision, trained female Fijian field assistants interviewed 70 mothers from randomly sampled households in three Yasawan villages – Bukama,

Dalomo, and Teci – about "pregnancy sickness" (nausea, vomiting, and related sensations). Twenty randomly selected female heads of households were also interviewed about the composition of their households' diets. The interviews were carried out in standard Fijian and subsequently translated to English before coding and analyses.

Additional information regarding the study site and the participants are provided in the supplementary materials (S Text 1).

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 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 and Sherman, 2000; Minturn and Weiher, 1984). One recent study investigated the development of novel food and olfactory aversions during pregnancy in two small-scale pastoralist societies from East Africa, (the Datoga and the Turkana - Young and Pike, 2012)but its authors did not

report any findings about other symptoms of NVP (Young and Pike, 2012). So, to our knowledge, our study provides the first quantitative evidence that NVP is a common feature of pregnancy in at least one small-scale, subsistence-level population.

Adult female volunteers were asked whether they had experienced any pregnancy sickness (called "*kune ca"* in standard Fijian) during their most recent 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. 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), irrespective of whether the women self-diagnosed as having *kune ca*.

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 their pregnancies. 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.

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 ("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. Further details on category selection and on how we combined the freelist and checklist data are provided in the supplementary materials (S Text 2.1-2.2).

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 but only 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%).

With regard to 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 experienced at least one novel food aversion during their pregnancies. Of the remaining 24 women, 22 (92%) experienced at

131 least one food aversion (although many of the aversion responses in these non-NVP
132 women were only invoked by the checklist questions, not by the freelist questions).

133 With respect to husband aversions, we found that 19 (41%) of the 46 Yasawan
134 women with NVP became averse to the smell of their husbands during their pregnancies.

135 [Table 1]

136 Thus, the data strongly suggest that NVP exists on Yasawa. The expression of
137 *kune ca* on Yasawa is consistent with how NVP has been described for other populations.
138 That is, nausea and vomiting often co-occur with one another and with some combination
139 of headaches, fatigue, dizziness, and the development of novel aversions, primarily
140 during the first three to four months of pregnancy (Firoz et al., 2010; Flaxman and
141 Sherman, 2000; Patil et al., 2012). Our main unexpected finding was that many Yasawan
142 women were strongly averse to the smell of their husbands during pregnancy; this
143 phenomenon has only been documented anecdotally previously (see Steinmetz et al.,
144 2012: p. 424).

145 Regarding our second objective for this section of our study – comparison of the
146 prevalence of NVP on Yasawa to global NVP prevalence rates for previously studied
147 populations – we used the diagnosed rate of 66% as the Yasawan rate. We then took
148 published prevalence rates for comparator populations from a meta-analytic study by
149 Pepper and Roberts (2006). The sample contained ten outlying data points, six of which
150 we excluded either because they reflected values based solely on vomiting prevalence
151 rather than total NVP prevalence or because they focused on a distinct subset of a
152 population (e.g. adolescent mothers, mothers with eating disorders, or mothers with

children that developed milk allergies). The other four outliers appeared reliable, so we retained them. Because the culled dataset contained only 11 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 and Eryilmaz, 2013), two from Tanzania (Nyaruhucha, 2009; Steinmetz et al., 2012), and two from Ecuador (Weigel et al., 2006; 2011). 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 SPSS 17.0.

We summarize cross-national variation in NVP prevalence in Figure 1. We found that Yasawa's NVP prevalence rate is not unusual in global perspective. In our updated version of the 2006 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%+/-0.17, with a median of 69%, and mode of 67%. The range of variation and the interquartile distance among the 16 non-Western countries (35%-90%) are slightly greater than that for the 39 Western countries (44%-90%), although the means of the two groups (respectively: 63%+/-4.19 and 70%+/-1.61) are statistically indistinguishable from one another (t=1.379, p=0.18). The Yasawan prevalence of 66% falls near the central tendencies of all of these ranges. These findings

suggest that NVP is expressed in the Yasawa Island population at a rate similar to those documented for larger scale populations.

[FIGURE 1]

Comparing the expression and prevalence of NVP on Yasawa Island to global prevalence highlights two points. First, NVP exists at a non-trivial rate in a small-scale society with a predominantly local diet. This result suggests that 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. Second, prevalence of NVP on Yasawa falls near the central tendencies for the global sample, the Western sub-sample, and the non-Western sub-sample. Although we cannot draw any strong inferences about whether small-scale societies in general tend towards the centre of the distribution with respect to NVP prevalence, this finding may hint that there may be some tendencies, across populations and across ecological circumstances, for about two-thirds of women to experience NVP. Additional studies should investigate whether the distribution of variation in NVP prevalence among a number of small-scale societies resembles the patterns observed in the global sample.

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 symptoms occur in contemporary populations.

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" (Fessler, 2002; Flaxman and Sherman 2000). This hypothesis is based on two well-understood features of pregnancy. One is that pathogens and teratogens can have particularly harmful, long-lasting impacts when an individual is exposed to them during embryo tissue differentiation, during the first 12 weeks of pregnancy (Carlson, 2004; Langley-Evans, 2006; Myatt, 2006; Rillamas-Sun, 2010). The other is that mothers down-regulate their immune functions during early pregnancy to facilitate the tolerance of embryonic tissues, which maternal immune systems would otherwise recognize as "non-self" and attack (Fessler, 2002; Svensson-Arvelund et al., 2013). This maternal immune suppression enables tolerance of embryos but also leaves both mothers and embryos vulnerable to pathogens and chemical toxins. The maternal-embryo protection hypothesis, then, holds that NVP is an adaptive solution to the problem of fetal and maternal vulnerability to pathogens and teratogens during early

pregnancy (Fessler, 2002; Flaxman and Sherman, 2000; see also Hook, 1976; 1978; Profet, 1988). The core assumption of this hypothesis is that mothers unconsciously compensate for their immunological vulnerability by developing novel aversions (often 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 (Coad et al., 2002; Huxley, 2000). This hypothesis suggests that mothers and embryos differ in their genetic interests in embryonic 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). Embryo fitness, on the other hand, generally benefits if the embryo avoids abortion and procures as many resources from its mother as possible without harming maternal (and therefore its own) survivorship (Haig, 1993; Trivers, 1974). So, embryos hormonally advertise their viability to reduce risk of abortion and to demand maternal resources. The compensatory placental growth hypothesis holds that one way in which 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 calorie-restricted mothers prioritize the allocation of energy to current reproduction through increased placental growth over the allocation of energy to future reproduction through fat storage

during early pregnancy (Huxley, 2000; Lunney, 1998; see also Weigel et al., 2006). Well-nourished mothers, in contrast, generally pursue strategies in which they 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 favour investment in their own development.

The "by-product of genetic conflict" hypothesis resembles the compensatory placental growth hypothesis 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 compensatory growth hypothesis 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 endrocrinology that trigger immune responses such as nausea or vomiting (Forbes, 2002).

As noted, the fourth and final approach to understanding NVP conceives of the symptoms as pathologies (Sherman and Flaxman, 2002). Although many of the proponents of this hypothesis acknowledge the puzzle of the observed negative correlation between the severity of NVP and risk of spontaneous abortion (Irving, 1940; Weigel and Weigel, 1989; Weigel et al., 2006), few offer functional or adaptive explanations for these phenomena and instead focus on pharmacological interventions that reduce or eliminate NVP symptoms (e.g. Anderka et al., 2011; Clark et al., 2012; Tan and Omar, 2011). The pathology approach to NVP does not seek to explain the existence

of NVP and therefore does not offer any 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 and Sherman, 2000; Sherman and Flaxman, 2002), we will not evaluate this hypothesis here.

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 maternal-embryo protection hypothesis, 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, bitter, or sour flavours (Fessler, 2002; Flaxman and Sherman, 2000; Patil et al., 2012). The maternal-embryo protection hypothesis 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 compensatory placental growth hypothesis, 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 nausea and vomiting are triggered by hormonal disturbances due to genetic conflict, predicts that women will experience nausea regardless of external triggers. If an episode of nausea co-occurs with an exposure to a particular food, a woman will learn an aversion to that food. So, this hypothesis predicts that whatever foods are most frequently encountered by a woman are those that are most likely to be associated with a conflict-related episode of nausea and thus are most likely to become aversive.

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. The food aversions data were taken from the same 70-woman interview 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 of the foods she had prepared for herself and her family the day prior to the interview and to report the quantity of each food she prepared.

We employed multiple 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. A summary of the hypotheses and their test predictions are presented in Table 2.

[TABLE 2]

We assigned each food category a pathogenicity and teratogenicity score between one and nine. Initial scores concerned pathogenicity only, and ranged between one and six. These pathogen scores were 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 how many Kg/ year each US citizen consumes of food from that category (from the Food and Agriculture Organization, United Nations, 2013's Food Balance Sheet for the US, 2006). To generate our overall measure of pathogenicity and teratogenicity, we added three additional points to the pathogen riskiness scores of each of the three food categories thought to contain chemical toxins (cassava; fish; and spicy/sour/bitter vegetables); zero points were added to categories not thought to contain teratogens. Complete details on the data sources and how we calculated these scores are provided in the supplementary materials (S Text 2.3).

To estimate the proportion of macronutrients – carbohydrates, protein, and fat – 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) approximate daily carbohydrate 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 macro- and micro-nutrient nutritional profiles for a wide variety of foods. In cases in which a Fijian food type was not represented in the 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 (cassava, dairy, fish, fruit, imported starches, local starches, meat,

mild-tasting vegetables; non-fish marine, oils and fats, and spicy/sour/bitter vegetables). 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.

Because women reported the quantities of household foods they prepared in units that were not easily comparable to one another, we lack a standardized measure of how often women are exposed to the foods in each food category. As such, we used the total caloric contribution of each food category to the average household diet as a proxy for encounter rate. These caloric yield estimates were also calculated using the Nutrient Database for Standard Reference (2012).

The results of the regression analysis are summarized in Table 3 and in the residual plots presented in Figure 2a-c. We found that the model accounts for ~56% of the variation in the number of women that are likely to become averse to a particular food category. Pathogenicity and teratogenicity score is the only significant predictor in the model, with a beta coefficient of 0.66, meaning that a standard deviation change in the Pathogen-Teratogenicity scores predicts a two-thirds of a standard deviation increase in the number of women who found it aversive. Rate at which women develop novel aversions to a particular food category was not significantly related to that category's macronutrient density or to its caloric yield.

[Table 3]

[Figures 2a, b, and c]

The regression results suggest the maternal-embryo protection hypothesis provides the best explanation for variation in the rate at which women develop novel aversions to a particular food category, at least in this population.

Furthermore, as mentioned previously, 19 (41% of women with NVP) of the women in the Yasawan sample reported novel aversions to the smell of their husbands. Fessler and colleagues (2005) predicted this finding, and it is consistent with the maternal-embryo protection hypothesis. Other people certainly constitute sources of contagion, and sexual or romantic partners may expose one another to pathogens through a particularly wide range of transmission mechanisms (Schaller and Murray, 2008). So, if women are experiencing NVP to protect themselves and their embryos during first trimester immuno-suppression, it is likely that they would be motivated to avoid a variety pathogen threats, including those potentially carried by their husbands and transmitted sexually. Notably, neither the by-product hypothesis nor the compensatory placental growth hypothesis provides a logically sound explanation for why women may be averse to their husbands' aroma during early pregnancy.

Taken together, then, the data from Yasawa Island support the maternal-embryo protection hypothesis. The Yasawa Island data do not support the compensatory placental growth hypothesis or the by-product of genetic conflict hypothesis.

DISCUSSION AND CONCLUSIONS

In the first part of the study reported here, we investigated the expression and prevalence of NVP on Yasawa Island, Fiji. 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. In the second part of the study, we used the Yasawa Islander data to test three evolutionary hypotheses for NVP – the maternal-embryo protection hypothesis, the compensatory placental growth hypothesis, and the by-product of genetic conflict hypothesis. 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 and spicy/sour/bitter-tasting plant foods. Unexpectedly, we also found that, during pregnancy, many Yasawan women develop aversions to the smell of their husbands. Given that other humans also represent potential sources of pathogen exposure, these findings support the maternal-embryo protection hypothesis but not the other two hypotheses.

Our study has a number of theoretical and practical implications, and indicates several routes for future research. With respect to the description of the expression of NVP on Yasawa, our study is among the first to differentially diagnose NVP and quantify its prevalence in a small-scale, subsistence-level population. Additionally, it is one of a relatively small number of 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). Given that the level of NVP prevalence on Yasawa Island is so close to the central tendencies of the global samples pertaining to NVP prevalence, it will be particularly interesting to see if other small-scale populations cluster near the centres of these global distributions. So, future work should seek to characterize NVP in other subsistence-level populations. Lastly with respect to this first part of our study, the interviews indicated that the pregnant 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 in at least one previous study (Steinmetz et al., 2012: p. 424). Future research on the women of 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 husbands are common in other socioecological contexts and, if so, under what circumstances such aversions arise.

Our evaluation of the evolutionary hypotheses for NVP highlights three important points. First, the finding that the data from the women of Yasawa Island are most consistent with the maternal-embryo protection hypothesis 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 (2002), Flaxman and Sherman (2000), Minturn and Weiher (1984), and Pepper and Roberts (2006) indicate that food aversions of pregnancy

421 focus preferentially on animal foods and that NVP prevalence is higher in populations in
422 which animal foods constitute a larger portion of the diet. Similarly, a series of within-
423 population studies in Ecuador, Kenya, Tanzania and the US suggest that, during early
424 pregnancy, women are relatively likely to develop aversions to meat and/or fish (Hook,
425 1978; 1980; Nyaruhucha, 2009; Olusanya and Ogundipe, 2009; Steinmetz et al., 2012;
426 Weigel et al., 2011). Given that most animal foods are more likely to contain non-
427 detectable biotoxins than most plant foods (Fessler, 2002; Fessler and Navarrete, 2003)
428 these within- and among- population patterns have generally been interpreted as support
429 for the maternal-embryo protection hypothesis. But, animal foods not only constitute
430 potential pathogen risks but also constitute high quality, nutrient-dense foods (Sailer et
431 al., 1985). The compensatory placental growth hypothesis suggests that, in calorie-rich
432 environments, embryos should manipulate their mothers to avoid such foods. So, many of
433 the key findings regarding aversions to animal foods or correlations between NVP
434 prevalence and contribution of animal foods to the diet can be interpreted as supporting
435 both the compensatory placental growth hypothesis and the maternal-embryo protection
436 hypothesis. Our study, however, quantitatively evaluated whether aversions were most
437 focused on foods high in pathogen and teratogen load or high in nutrient density, and
438 found evidence that pathogenicity and teratogenicity are the strongest predictors of food
439 category aversiveness. These results offer support for previous interpretations of evidence
440 regarding aversions to animal foods that suggest that such foods are especially aversive to
441 pregnant women because of their possible toxicity rather than their nutrient density. They
442 also highlight the need for additional studies in other populations that take both the

443 quality and the pathogenicity of animal foods into account when testing hypotheses for
444 NVP.

445 Second, regardless of the selective mechanism for the evolution of NVP, the
446 evidence from Yasawa supports the notion that NVP represents a suite of evolved
447 characters rather than a set of pathological symptoms, offering further justification for
448 rejecting the pathology hypothesis for NVP. That is, Yasawan women avoid foods and
449 develop NVP in the patterns predicted by one of the evolutionary hypotheses and these
450 patterns would be difficult to explain if NVP were pathological. Our finding that food
451 aversions during pregnancy on Yasawa are strongly patterned is in keeping with a
452 growing corpus of data from a wide variety of other studies (see recent review by Patil et
453 al., 2012).

454 Lastly, our finding that NVP may serve to protect mothers and embryos from
455 pathogens and chemical toxins has implications for clinicians and for future researchers.
456 As it is currently unclear whether managing NVP negatively impacts fetal health and
457 survivorship (Flaxman and Sherman, 2000; Nulman et al., 2009; Sherman and Flaxman,
458 2002; Tan and Omar, 2011), future studies should focus on whether NVP continues to be
459 adaptive with the emergence of an industrial food system, including refrigeration,
460 standardized processing of plants containing toxic compounds, and food labels. As this
461 body of research grows, clinicians will be better equipped to recommend whether or not it
462 is safe to repress NVP in environments in which pathogen and teratogen threats can be
463 avoided in other, less uncomfortable ways. We also suggest that viewing NVP as
464 adaptive rather than pathological may require using different language than what has
465 previously been used in clinical literature. In particular, describing NVP as a “syndrome”

466 or a “set of symptoms” implies that it is a pathology. Yet, we find that nearly all Yasawan
467 women experience at least one new and temporary food aversion during pregnancy. So,
468 future work that treats NVP as an adaptation should perhaps use the more neutral
469 vocabulary of evolutionary biology and describe NVP as the expression of one or more
470 behavioural and physiological traits.

471

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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 *Kune ca*	47	67%

Caption for Fig 1

Figure 1: Boxplots of cross-national variation in NVP prevalence. The Yasawa Islanders of Fiji are shown between prevalence rates from populations from Western and Non-Western countries.

Figure 1

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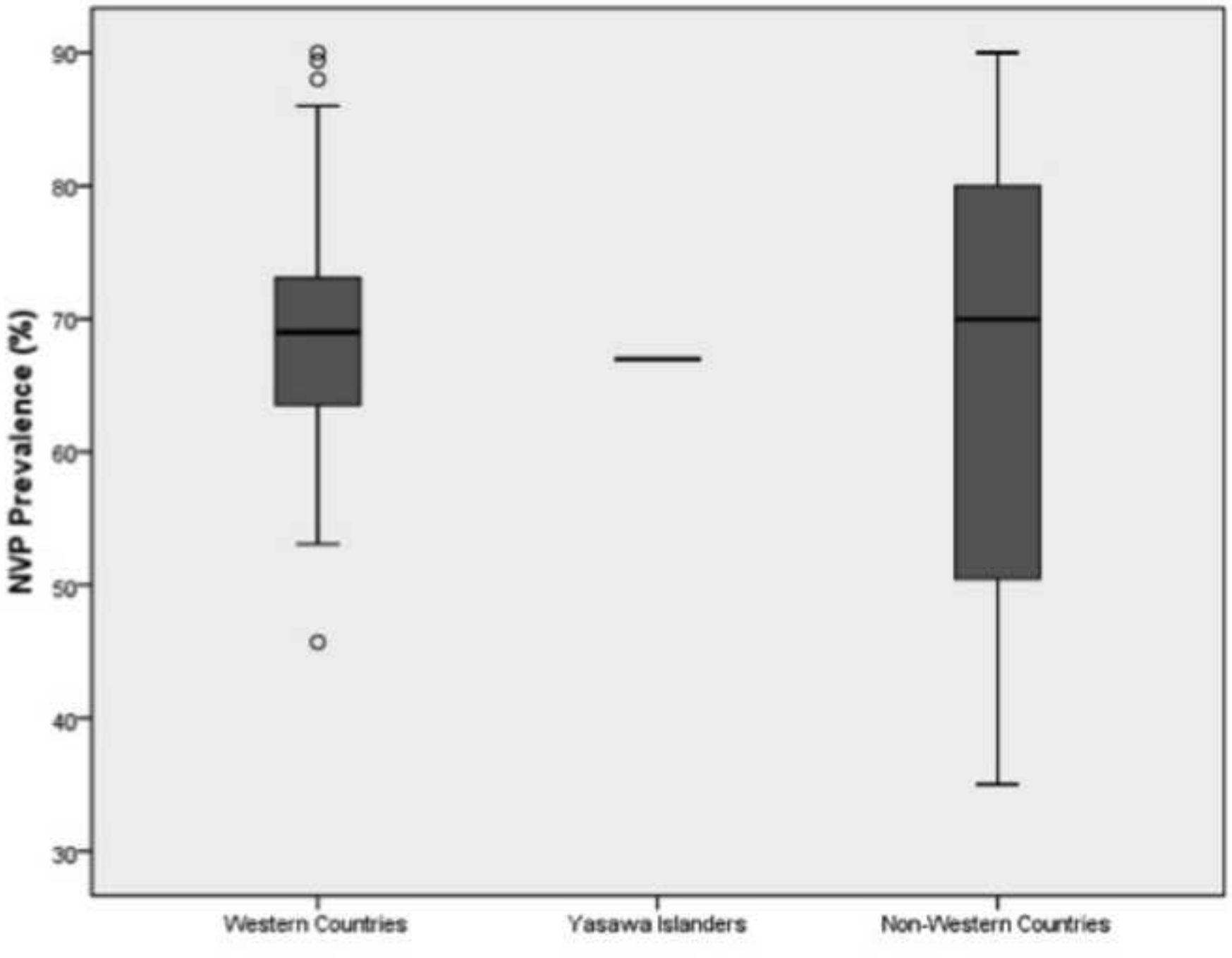

Table 2: Hypotheses for the evolution of NVP and their predictions regarding foci for novel aversions during pregnancy.

Hypothesis	Test Predictions
Maternal-embryo protection	• Rate at which women develop novel aversions to a particular food category correlates positively with the pathogenicity and teratogenicity of that category • Women may develop aversions to other key non-food sources of pathogens or teratogens
Compensatory placental growth	• Rate at which women develop novel aversions to a particular food category correlates positively with the macronutrient density of that category
By-product of genetic conflict	• Rate at which women develop novel aversions to a particular food category correlates positively with rate at which women encounter that category

Table 3: Results from regression of number of women with aversions to a particular food category on possible predictors of that food category's aversiveness.

Predictor	β	***p***
Pathogenicity and teratogenicity risk score of food category	0.659	0.036
Score of food category's contribution to macronutrient composition of normal household (non-pregnancy) diet on Yasawa Island	0.289	0.371
Caloric contribution of food category to normal household (non-pregnancy) diet on Yasaw Island	-0.058	0.829

Caption for Fig 2

a
b
c
FIGURE 2: Relationships between rates at which women develop novel aversions to food categories and characteristics of those food categories. 1a. Partial correlation plot of rate of food category's aversiveness and its pathogenicity and teratogenicity risk score. 1b. Partial correlation 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. 1c. Partial correlation plot of rate of food category's aversiveness and its caloric contribution to the regular household (non-pregnancy) diet on Yasawa Island.

Figure 2a

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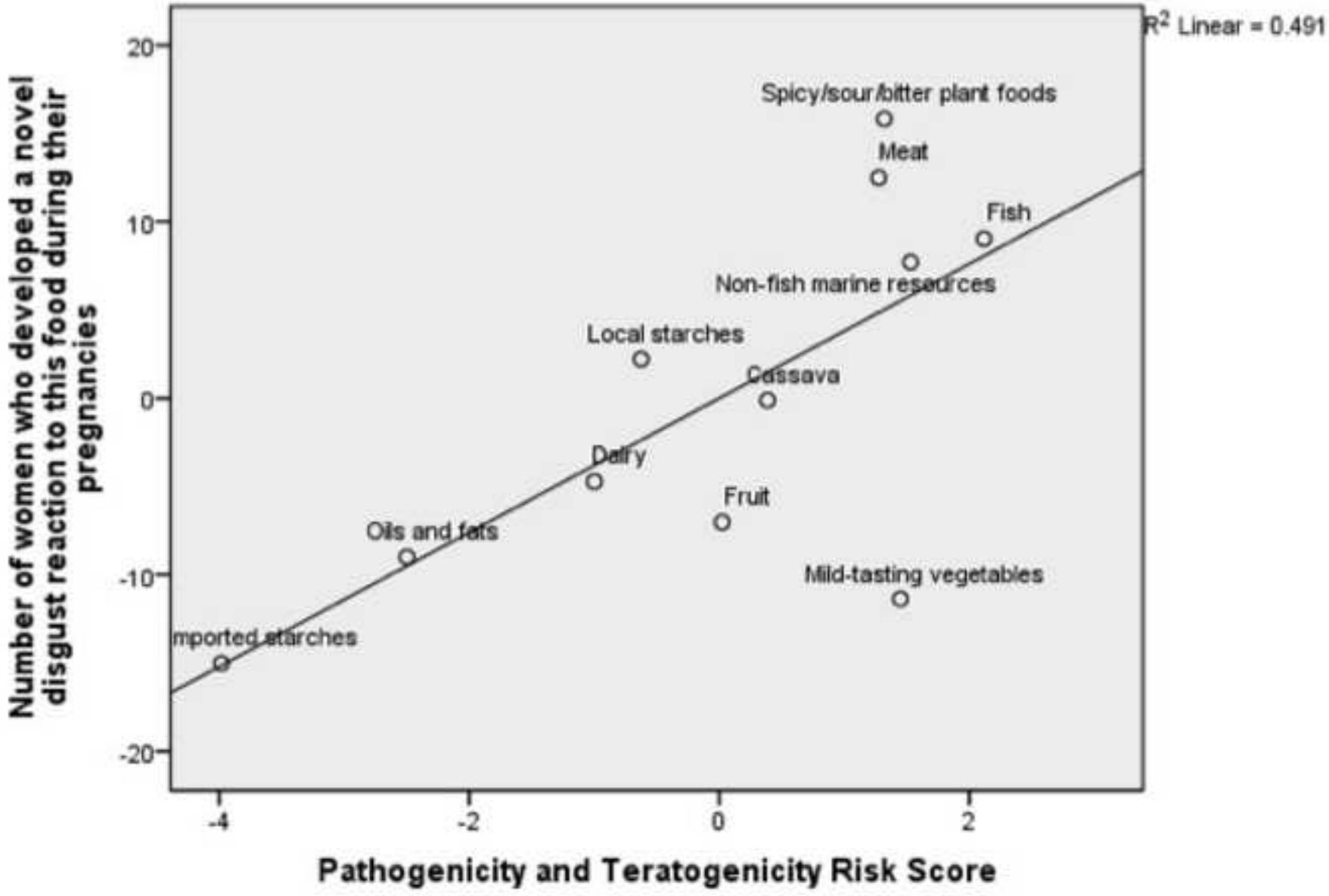

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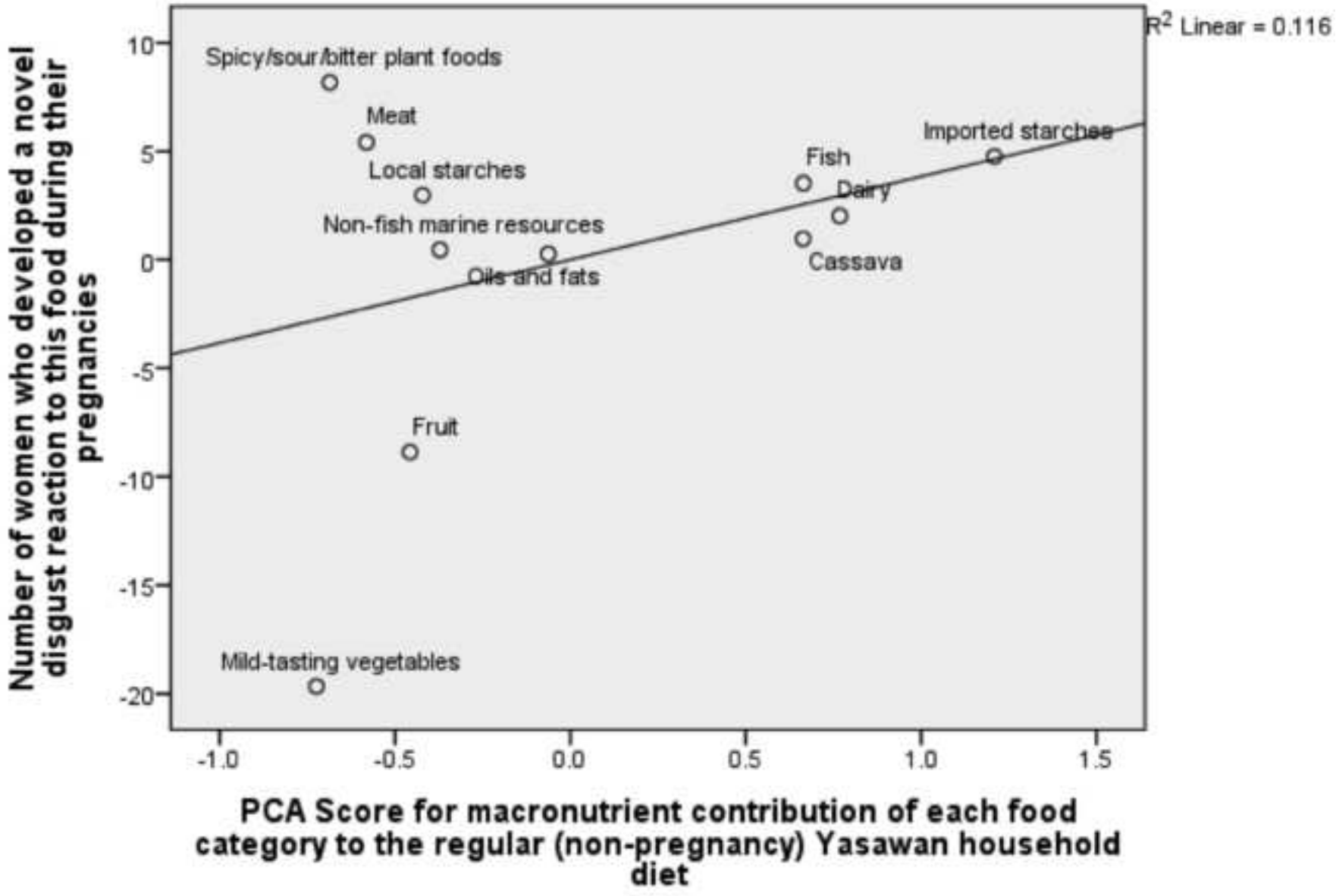

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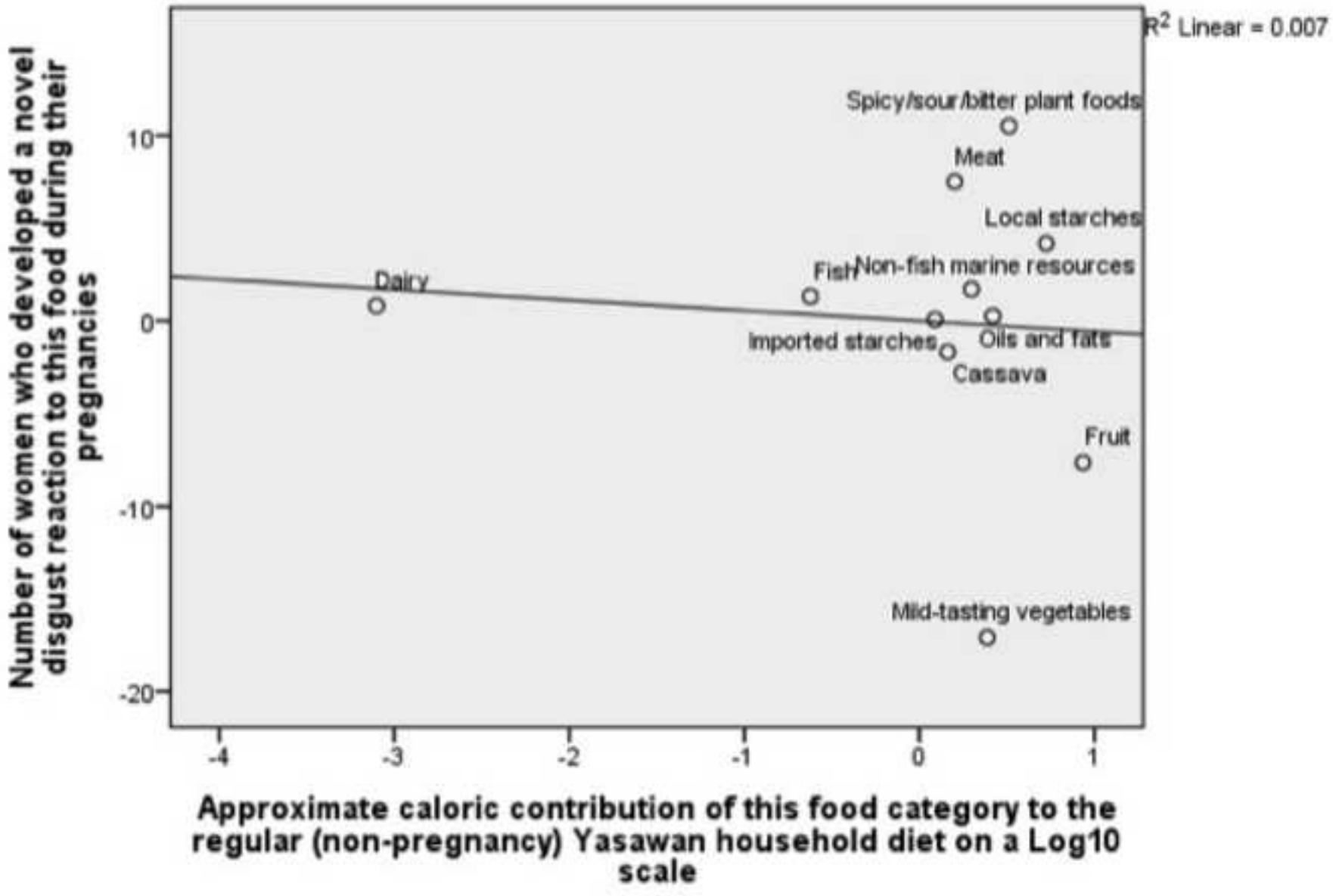

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