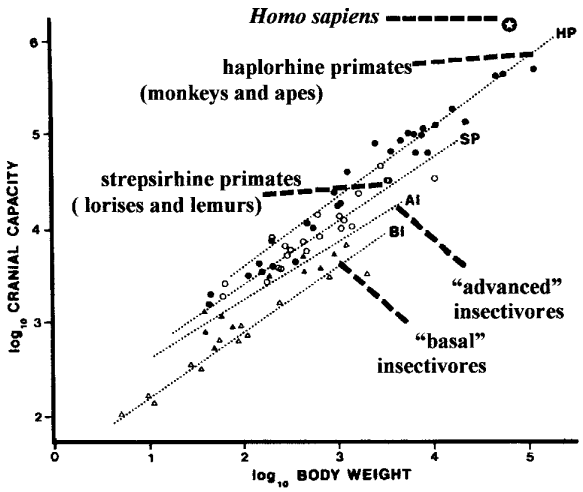

FIG. 2. *Allometric relationships between cranial capacity and body weight in different categories of primates and some other mammals (after Martin 1983).*

aptation to energy-rich foods that is also apparent in the divergence from the allometric prediction computed from a teleost sample that probably includes species with various diets. In contrast, a species that grazes on plants does not need to be clever (except to escape predators), and the large gut of *Hypostomus plecostomus* is a necessary adaptation to a vegetarian diet with no direct relationship to brain size.

In any case, Kaufman is to be commended for not hesitating to bring the fishes into the field of anthropology. Although they do not provide an adequate model for encephalization, fish studies may allow us to understand other aspects of primate (and human) adaptations. This is especially true for sensory perception, given that some fish species perceive tastes through their whole skin and that our fish origins are important in explaining why we can detect a salty taste (Hladik, Simmen, and Pasquet 2003). The large mormyrid brain is presumably adapted to a world of sensory perceptions unknown to humans in relation to detecting electrical fields that involve the encoding of a large amount of information.

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On Morning Sickness and the Neolithic Revolution[1]

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A topic that has been long been of interest to anthropologists, neurobiologists, and reproductive biologists is nausea and vomiting in pregnancy (NVP), commonly referred to as "morning sickness." NVP was first reported by the Greeks nearly 4,000 years ago (Fairweather 1968), but until recently it was difficult to judge its prevalence outside the Western world. We now know that NVP is more or less ubiquitous, although its frequency of occurrence varies considerably across populations (Fessler, CA 43:19–61; Flaxman and Sherman 2000). Hence the real question: Since it is axiomatic that a pregnant woman must "eat for two," why should a condition that restricts food intake occur at the same time as this dramatic rise in nutritional and caloric requirements? One possibility is that NVP is linked to an evolutionary advantage, and indeed it has been shown that women who experience NVP are significantly less likely to miscarry than women who do not (Petitti 1986, Weigel and Weigel 1989).

Along these lines, much of the current research on NVP has focused on the potential role of nausea and vomiting in protecting an individual from the harmful effects of ingested toxins and the pathogens that produce them. In a pregnant woman, those toxins and pathogens

1. We thank S. M. Flaxman, P. W. Sherman, and M. Profet for extremely helpful comments on an early draft.

put two humans at risk. Therefore, a condition that protects a pregnant woman and thus her fetus from harmful substances should confer an adaptive advantage. The curious feature of NVP is that many pregnant women experience nausea and vomiting *before* ingestion. As Fessler (CA 43:19) points out, the "striking differences between the circumstances of normal nausea and vomiting and those of pregnancy . . . sickness call for explanation." To this end, he has examined 73 societies in the Human Relations Area Files to determine if there were cross-cultural patterns in the kinds of foods targeted by taboos. His findings, which mirror those of other investigators (e.g., Dye, Jones, and Hill 1998, Flaxman and Sherman 2000, Knox, Kremer, and Pearce 1995), clearly demonstrate that meat is the principal target of aversion. Fessler proposes (p. 20) that "a principal function of pregnancy sickness is the provision of prophylactic protection from meat-borne pathogens during reproductive immunosuppression." In plainer terms, "morning sickness causes women to avoid foods that might be dangerous to themselves or their embryos, especially foods that, prior to widespread refrigeration, were likely to be heavily laden with microorganisms and their toxins" (Flaxman and Sherman 2000:113).

This explanation is similar to one proposed by Profet (1988, 1992), following research by Hook (1976, 1978, 1980). The idea is that NVP protects the fetus primarily from secondary compounds produced by plants as defensive agents. These compounds contain teratogenic and abortifacient chemicals, but an evolved tendency to avoid these agents or to expel them through vomiting reduces the incidence of fetal mortality. In Profet's model, NVP first evolved during the Pleistocene (ca. 11,000 years ago) to discourage "first-trimester pregnant women from experimenting with novel toxic foods, in favor of incurring short-term nutritional costs and sustaining viable embryos" (1988:180). To this end, "periods of scarcity would have provided the greatest selection pressures for pregnancy sickness."

Lost in various models is the fact that whereas there is a documented reproductive advantage associated with NVP, *any* reproductive advantage will be negated if the pregnant woman suffers significant dietary hardship as the result of her culture's settlement-subsistence pattern. We contend that periods of food scarcity would have provided the greatest selection *against* NVP, whether the advantage was a physiological process, simply a side effect of some hormonal level, or a fetal-protective mechanism of the type proposed by Profet, Fessler, and Flaxman and Sherman.

Any model that correctly explains NVP in adaptive terms must be capable of integrating biology and culture. We propose the following model: Under conditions of no ecological or dietary stress, a reproductive advantage is to be had by women experiencing NVP relative to pregnant women lacking the condition. (Hyperemetic mothers are always at a disadvantage because of the severity of the condition.) As stress—especially dietary stress—increases, women with NVP lose their reproductive edge over women not experiencing nausea if for no other reason than that they are less able to use (scarce) food resources. Thus, selection will favor a pregnant woman with the requisite conditions for NVP *only* if dietary and other forms of stress have been reduced. We posit that the evolution of cultural practices that ease stress on a pregnant woman with NVP should increase the overall fitness of the group possessing those practices. Even in modern Western cultures, little can be done for NVP except to alleviate the symptoms through the generally prescribed regimen of small, frequent meals of easily digested carbohydrates (cooked cereal often being the best tolerated), avoidance of fat- and protein-laden foods, and a reduction of activity. These may appear to be relatively "easy" cultural adjustments, but none would be possible if it were not for changes associated with the shift from food procurement to food production that began approximately 10,000 years ago.

The "Neolithic Revolution" is characterized by an increasing dependence on domesticable foods and the process of sedentarization. With certain exceptions, early plant domesticates were carbohydrate-rich: potatoes in South America, maize in Middle America, starchy seeds in the American Midwest, cereal grains in the Near East, and rice in Southeast Asia. Certainly foods containing carbohydrates were present prior to 10,000 years ago, but it is important that through time humans developed intensified relations with carbohydrate-rich plants to the point that such plants became staples of the human diet. Not only are carbohydrate-rich foods readily stored, but when cooked they are easily digested and can be tolerated by a nauseated woman. Interestingly, Flaxman and Sherman (2000) found that compared with societies in which morning sickness was observed, societies in which it was not observed were significantly more likely to have *only* plants as staples (as opposed to meat and fish), with maize often serving as the *only* staple. A maize-based diet lacks essential amino acids, but this can be overcome by either alkali processing of the maize or the addition of plants such as lysine- and tryptophan-rich legumes to the diet.

We know that a strong correlation exists between the tolerance of certain foods and their culturally based restriction during pregnancy. Thus what appear at first glance to be "allegedly irrational and harmful" food taboos (Harris 1987:67) are in reality cultural adjustments to what a pregnant woman should and should not eat. For example, meat and fish are withheld from pregnant Murngin women as soon as they cease to menstruate; thereafter their diet is limited to grass seeds, yams, the fruit of the cycad, some shellfish, and crabs (Mountford 1956). In parts of the Tamil-speaking region of India (Ferro-Luzzi 1980:101), "women in the first months of pregnancy are prone to vomiting," and therefore "expensive flesh should be denied so that it might not be wasted." Thus the frequent occurrence of "taboos, superstitions, and prohibitions that serve to eliminate or reduce potential sources of protein from the diet of menstruating, pregnant, or lactating women" (Wood 1979: 154) is not surprising, given that either the foods could not be digested in the first place or, as Flaxman and Sher-

man (2000) and Fessler (CA 43:19–61) suggest, NVP is an evolved tendency to protect a woman and her fetus. The selective advantage of NVP, however, depends in large part on the availability of a replacement food.

But ease of digestion is only one component of an integrated cultural adaptation. Concomitant with, although not restricted to, increased use of carbohydrate-rich plant foods in many parts of the world was a general increase in sedentism (Sussman 1972). An increase in sedentism, even if slight, can have a tremendous impact on pregnant women (not to mention facilitating the storage of food against future lean times). The pronounced fatigue commonly associated with the first trimester of pregnancy—especially when aggravated by a lack of interest in food and/or the inability to retain food—could make even the shortest journey an ordeal. (This fact has seemingly been overlooked by many deskbound demographers.) In addition, an increase in fertility—facilitated by a shift to carbohydrate-rich foods—may have resulted in more children at home (Buikstra, Konigsberg, and Bullington 1986, Holland 1989). Older children would have been able to shoulder some of the mother's workload and thus reduce her activity (Dumond 1975). Technology to process and store these foods (e.g., pottery and alkali processing) developed in tandem.

Therefore, while we agree with Flaxman and Sherman (2000) and Fessler (CA 43:19–61) that NVP is an evolved tendency to protect a woman and her fetus, we contend that the selective advantage of NVP is dependent on a complex web of adaptive responses. We suggest that the frequency and geographic distribution of NVP can be explained only by examining broad evolutionary change in the cultural and physical environments that began 10,000 years ago. These changes blunted selection's heavy toll on women and the children they carried. As a result, a reproductive advantage associated with the maternal propensity for NVP could be realized. Changes brought on by the evolution of food production have made it easier to mitigate the stress that rendered NVP disadvantageous. As a result, morning sickness is typically regarded as nonlife-threatening in modern populations. Although at term (in modern Western populations) there are no differences in infant birth weight between infants from mothers with NVP and those from mothers without NVP, we suggest that this has not always been the case. A mother subjected to periodic food deprivation as a consequence of her culture's settlement-subsistence pattern might not be able to recover from even a relatively minor (additional) insult such as NVP. We clearly cannot extrapolate the "harmlessness" of NVP in modern populations to the past. Morning sickness, while a nuisance to Western mothers, is harmless given proper food and obstetric care, but few will argue that modern medical and nutritional knowledge evolved at the same rate as human physiology.

Thus, morning sickness may not be a direct consequence of Western civilization as Dieckmann (1938) proposed a half-century ago, but certainly changes in food production have contributed to its widespread distribution and frequency of occurrence. Although not technically a disease, NVP nonetheless may have to be added to the list of conditions that some (e.g., Eaton and Konner 1985) believe includes obesity, diabetes, hypertension, and some forms of cancer—all of which may be linked to dietary shifts that occurred in the recent past.

Reply

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Holland and O'Brien's thought-provoking extension of the idea that pregnancy sickness[2] protects both the mother and the developing organism[3] from ingestible pathogens and toxins during a period of enhanced vulnerability has a number of important difficulties.[4]

First, it assumes that the dietary constriction entailed by pregnancy sickness constituted a significant cost to ancestral foragers. However, as I have pointed out (CA 43:26), the first trimester of pregnancy, the period during which pregnancy sickness is most marked, is characterized by notably low caloric demands. While adequate protein intake is important during pregnancy, this is principally true of the second and third trimesters (see CA 43:28). Therefore, although any mechanism that results in dietary constriction entails costs, it is important not to overestimate the impact of enhanced first-trimester dietary selectivity if we want to assess the strength of the stabilizing selection that limited the extent and/or prevalence of pregnancy sickness in ancestral forager populations. Moreover, even if we entertain their premise, the facts do not support Holland and O'Brien's conclusion that the Neolithic Revolution reduced the costs of pregnancy sickness.

Holland and O'Brien argue that changes in the relative nutritional and caloric costs of pregnancy sickness resulting from the domestication of plants partly explain the "frequency and geographic distribution" of the trait. They reason that the more domesticated plant foods can be substituted for the game animals and wild plant foods on which foragers rely, the less costly it is to avoid pathogen- and toxin-bearing wild foods and hence the more advantageous such avoidance becomes. Pregnancy sick-

2. Although they follow Flaxman and Sherman (2000) in referring to the syndrome at issue as "nausea and vomiting of pregnancy (NVP)," the term "pregnancy sickness" more accurately captures the suite of physiological, subjective, and behavioral changes characteristic of the first trimester of pregnancy.
3. Holland and O'Brien state that, during pregnancy, "toxins and pathogens put two humans at risk." Describing an embryo or first-trimester fetus as a human being is a political claim rather than a scientific portrayal. The use of such language obscures the delimited nature of the fitness value to the mother of an organism in which maternal investment to date is still relatively low.
4. I thank Guillermo Algaze (helpful source of information) and Jennifer Fessler (muse).

ness is the means whereby avoidance of foods hazardous to the mother and the developing organism is realized, and therefore it should be most evident in populations with the greatest reliance on domesticated plants.[5] However, the evidence they adduce suggests that the opposite is true. They note that (*a*) societies in which pregnancy sickness is apparently *absent* rely on plant staples, typically maize, and (*b*) maize can be processed in a way which enhances the availability of essential amino acids. If, as they argue, cultural innovations such as the domestication of maize and the development of maize-processing techniques involving alkali changed the selective forces acting on women so that "a reproductive advantage associated with the maternal propensity for [pregnancy sickness] could be realized," then why is pregnancy sickness both quite evident in foragers with no known history of agriculture (e.g., Shostak 1981) and least evident in exactly those agricultural societies in which it is ostensibly least costly and therefore most advantageous? Such a seemingly perverse outcome is understandable if Holland and O'Brien have misconstrued the changes brought on by the Neolithic Revolution.

Holland and O'Brien claim that the domestication of plants decreased the costs of pregnancy sickness by improving the nutritional status of women. However, the available evidence indicates that the rise of agriculture often taxed pregnant women by causing a net decline in nutritional status, in part because the adoption of agriculture ultimately led to a decrease in dietary breadth (Kiple and Tarver 1992, Sciulli 1977). This decline was likely exacerbated by the increased patriarchy facilitated by sedentism and agriculture (Whyte 1978), as this enhanced men's ability to monopolize the most desirable foodstuffs (cf. O'Laughlin 1974).

Holland and O'Brien propose that the domestication of plants diminished the costs of pregnancy sickness via reductions in energy expenditure achieved through sedentism. However, plant domestication probably exacerbated the exogenous energetic demands placed on women during the first trimester of pregnancy. While sedentism does eliminate the need for periodic relocation of a woman's home base, this energy savings is likely vastly overshadowed by the increased demands on female labor associated with both the rise of patriarchy and the dramatically increasing returns obtainable from intensification that agriculture, unlike foraging, supports (see Boserup 1990). To quote one of the sources cited by Holland and O'Brien, "It is clear that female work-related pathology changed significantly . . . in a way that would be consistent with a model of increased labor for women with the acquisition of maize agriculture" (Buikstra, Konigsberg, and Bullington 1986:531).

While the heightened fertility associated with the adoption of agriculture does allow women to delegate some chores to older children, any resulting energy savings are probably greatly outweighed by the elevated rates of maternal depletion caused by reduced birth intervals (see King 2003 for review). The increases in fertility associated with agriculture likely usually derive not from enhanced prosperity but from regionally variable combinations of (*a*) the greater value of children's labor, (*b*) the role of family size in the acquisition and defense of fertile land, (*c*) elevated infant and child mortality due to diseases associated with increased population density, and (*d*) the availability of weaning foods that shorten lactational amenorrhea (Armelagos, Goodman, and Jacobs 1991, Boserup 1990, Buikstra, Konigsberg, and Bullington 1986, Cowgill 1975, Kiple and Tarver 1992).

The shift from foraging to agriculture may have reduced the frequency of food shortages, but it likely also increased their severity. Domestication involves a reduction in plant defenses and an increase in the within-species simultaneity of ripening (Schwanitz 1966), changes that make plants more vulnerable to pests. Agriculturalists rely on a small number of staple crops, degrading or displacing alternative resources in the process. In contrast, foragers exploit a wide range of well-adapted food sources that exist in a complex, heterogeneous ecosystem and, consequently, are generally markedly less vulnerable to famines caused by pests and climatic variation (Armelagos, Goodman, and Jacobs 1991), exactly the type of events during which natural selection operates most intensely.

Perhaps the domestication of plants did change the distribution and frequency of pregnancy sickness, but any such change was probably in the opposite direction from that claimed by Holland and O'Brien. Whether via changes in allele frequencies or a reduction in facultative trait expression, because the adoption of agriculture increases the costs of pregnancy sickness it may reduce rather than increase its frequency. This conclusion is supported by the very study cited by Holland and O'Brien; 86% of the societies in which pregnancy sickness reportedly does not occur rely exclusively upon plant staples (Flaxman and Sherman 2000:131, table 3).[6]

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5. Holland and O'Brien repeatedly suggest that between-population differences in the prevalence and/or severity of pregnancy sickness are the product of differing selection pressures stemming from the respective means of subsistence. While this position is vulnerable to the criticism that gene flow may have disrupted any such culturally generated differences in allele frequency, the basic argument can be rescued simply by positing that these differences reflect facultative adjustment of trait expression in response to environmental contingencies. However, even this watered-down version of their position is contradicted by the facts that Holland and O'Brien themselves adduce.

6. Support for the facultative-adjustment explanation comes from the fact that two of the six cultures in which (*a*) pregnancy sickness is reportedly absent and (*b*) only plant staples are relied upon are Old World maize cultivators (Flaxman and Sherman 2000:130, table 2). Given that maize is a New World crop, it is extremely unlikely that selection could have altered allele frequencies in the fewer than 20 generations that have elapsed since the Columbian period.

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