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Proc. R. Soc. B published online 28 July 2010
doi: 10.1098/rspb.2010.1191

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FirstCite® e-publishing

Proc. R. Soc. B
doi:10.1098/rspb.2010.1191
Published online

The evolution of cultural adaptations: Fijian food taboos protect against dangerous marine toxins

Joseph Henrich[1,2,*] and Natalie Henrich[3]

[1]*Department of Psychology, and* [2]*Department of Economics, University of British Columbia, 2136 West Mall, Vancouver, Canada V6T 1Z4*
[3]*Centre for Health Evaluation and Outcome Sciences, Providence Health Care Research Institute, University of British Columbia, Vancouver, British Columbia, Canada V6Z 1Y6*

The application of evolutionary theory to understanding the origins of our species' capacities for social learning has generated key insights into cultural evolution. By focusing on how our psychology has evolved to adaptively extract beliefs and practices by observing others, theorists have hypothesized how social learning can, over generations, give rise to culturally evolved adaptations. While much field research documents the subtle ways in which culturally transmitted beliefs and practices adapt people to their local environments, and much experimental work reveals the predicted patterns of social learning, little research connects real-world adaptive cultural traits to the patterns of transmission predicted by these theories. Addressing this gap, we show how food taboos for pregnant and lactating women in Fiji selectively target the most toxic marine species, effectively reducing a woman's chances of fish poisoning by 30 per cent during pregnancy and 60 per cent during breastfeeding. We further analyse how these taboos are transmitted, showing support for cultural evolutionary models that combine familial transmission with selective learning from locally prestigious individuals. In addition, we explore how particular aspects of human cognitive processes increase the frequency of some non-adaptive taboos. This case demonstrates how evolutionary theory can be deployed to explain both adaptive and non-adaptive behavioural patterns.

Keywords: cultural transmission; dual inheritance theory; prestige bias; Fiji; food taboos

1. INTRODUCTION

In the last three decades, the application of evolutionary theory to understanding the origins and nature of social learning has generated a variety of insights into the behaviour of humans and other animals [1,2]. Theoretical work has illuminated both the ways in which natural selection has shaped human capacities for social learning [3] as well as how those capacities can, over generations, give rise to culturally evolved adaptations—that is, to yield complex, culturally transmitted, behavioural repertoires that address local environmental challenges [4,5]. While field research has long documented the intricate and often subtle ways in which culturally transmitted beliefs and practices adapt people to their environments, and experimental work in the laboratory has demonstrated the predicted patterns of social learning in both children and adults, little research has connected the actual adaptive repertoires observed in human societies directly to the predicted patterns of cultural transmission.

Addressing this gap, we first show that Fijian food taboos for pregnant and lactating women selectively target the most toxic marine species, effectively reducing a woman's chances of experiencing fish poisoning by 30 per cent during pregnancy and 60 per cent during breastfeeding. Next, we trace the pathways of cultural transmission. Consistent with certain existing evolutionary models of culture, our empirical findings suggest that these taboos are transmitted and sustained by a combination of familial transmission and selective cultural learning from senior women who are considered particularly successful, knowledgeable and prestigious. Beyond the adaptive repertoire, we also examine how certain reliably developing aspects of human cognitive processes may, as by-products, sustain positive frequencies of taboos on specific kinds of non-toxic foods. Overall, these results provide a detailed example of how evolutionary approaches can be deployed to explain both the adaptive and non-adaptive patterns in behavioural domains influenced by social learning.

* Author for correspondence (joseph.henrich@gmail.com).

Electronic supplementary material is available at http://dx.doi.org/10.1098/rspb.2010.1191 or via http://rspb.royalsocietypublishing.org.

2. THEORETICAL BACKGROUND

Numerous cases suggest that many of the practices found in human societies appear functionally well-designed to address local environmental challenges, often in ingenious ways not recognized by the people themselves. For example, Katz *et al.* [6] show how Native American populations incorporated an alkali, in the form of lye, ash or lime, into their maize cooking procedures in a manner that balances the essential amino acids and frees the otherwise unavailable niacin. Without such procedures, maize-dependent populations would face widespread malnutrition, including niacin deficiency (pellagra) and a lack of certain essential amino acids. Similarly, elaborate processing techniques protect foraging and horticultural populations [7–10] from the toxins present in otherwise valuable food sources (e.g.

Received 4 June 2010
Accepted 5 July 2010

acorns, cycads, cassava). Finally, research indicates that widespread practices involving the use of pathogen-killing spices in meat preparations protect people in warmer climates from food-borne illnesses [11]. Some of these authors have speculated on precisely the kind of cultural evolutionary processes that we provide empirical evidence for below (e.g. [12]).

While adaptive practices such as those described above are common across human societies, theoretical and empirical work are just beginning to illuminate how these practices emerge and are sustained. Evolutionary models explore how natural selection shapes the social learning abilities that lead individuals to selectively focus their attention on those people (models) most likely to possess adaptive information (e.g. beliefs, skills, practices). By preferentially attending to older models possessing cues indicating greater skill, knowledge, success, prestige and health, as well as to those with cues of self-similarity (like sex and ethnicity), learners can triangulate in on and preferentially learn from those most likely to possess fitness-enhancing practices, beliefs and values that will be suitable to the learner's likely future social roles [13]. However, accessing and learning from such preferred models may often carry non-trivial costs, as the model may not live nearby or may demand compensation for access. Under such conditions, learners should first acquire as much as they can from any available low-cost models (e.g. parents, siblings), who are readily available and have incentives (e.g. kinship) to permit social learning. Then, with this foundation, learners can decide whether to update their beliefs and practices with information acquired from their preferred models [14,15].

Building on this foundation, models of cultural evolution show how these adaptive processes give rise to population-level patterns of adaptation. If some members of every generation tend to use model-based cues to preferentially learn from the more successful, skilled and healthier members of the previous generation, the population-level distributions of beliefs and practices will evolve to an equilibrium that maximizes the success, skill and health of members (approximating optimal fitness)—giving rise to emergent culturally evolved adaptive repertoires [3,5,16].

When the population is far away from the optimal repertoire (the equilibrium favoured by selective imitation), a learner's low-cost models (family members) will often lack the adaptive beliefs and practices possessed by highly successful and prestigious individuals, leading to substantial cultural transmission from these higher cost models. Selective attention to preferred models will drive the population over generations towards the optimal repertoire. However, when this cultural evolutionary process is *at or near equilibrium*, adaptive learners will learn *mostly* from family members (at low cost), and will often not need to update from preferred models (e.g. particularly prestigious individuals) because mostly everyone else in the community will believe the same things as one's family.[1] Unless deviations from the optimal repertoire have a big impact on fitness such that natural selection can act on cultural variation to sustain the equilibrium, purely parent-to-offspring cultural transmission cannot maintain such behavioural adaptations because any noise or error in the transmission process will accumulate over time and drive the population away from the optimal repertoire. However, if a small fraction of learners still update by learning from preferred models, populations can remain at or near the optimal repertoire.[2]

This single strategy, of copying one's parents (family) and then updating from the wider world if others are both doing better and something different from one's family, may explain the variation between the emphasis on parent–offspring transmission observed in traditional (at equilibrium) domains in small-scale societies [17,18] and the emphasis on non-vertical transmission (not near equilibrium) in industrialized societies [19]. The electronic supplementary material provides additional discussion on this.

Empirically, a substantial laboratory research supports the above lines of theorizing by demonstrating that learners do indeed use cues of skill, success, prestige, sex and age to figure out whom to pay attention to and learn from across a wide range of domains [20,21: ch. 2, 22]. Recent experimental work with children has underscored these adult findings, by showing how children use subtle cues of competence, reliability, performance, prestige and intent [23–25] to figure out whom they will attend to and learn from. Field studies on topics ranging from food taboos and the diffusion of innovations to suicide and celebrity advertising suggest that these findings are relevant outside the laboratory [13,26]. No work, to our knowledge however, has yet connected the dots by showing that adaptive repertoires at the population level result from the predicted patterns of transmission at the individual level.

3. FIJIAN FOOD TABOOS

We studied food taboos during pregnancy and lactation in three villages on Yasawa Island, one of the outer islands in Fiji. Taboos (*tabu* in Fijian) are culturally transmitted prohibitions, the violation of which is perceived to carry social or supernatural sanctions (see the electronic supplementary material). After introducing the study population, we show that (i) marine toxins pose an important local adaptive challenge, (ii) food taboos during pregnancy and lactation differentially target toxic species, thereby potentially protecting foetuses and nursing infants, (iii) pregnant and breastfeeding villagers experience lower rates of fish poisoning than the same women at other times, and (iv) food taboos are culturally transmitted in patterns consistent with the above theoretical predictions, and thus in a manner that can explain their emergence and stability. Having addressed the consensus taboos in this population, we then explore how aspects of human cognition may explain the presence of some non-adaptive food avoidances reported by a non-trivial minority of the population. In each section, we introduce the issue, present the data-collection methods and move directly into the results and discussion.

The findings presented here were collected as part of an in-depth study of life on Yasawa Island, which lies in the north western corner of the Fijian archipelago (see the electronic supplementary material). Economically, villagers rely primarily on horticulture, fishing and littoral gathering. Yams and cassava provide the caloric staples, while reef fishes are the primary source of protein. Political units are composed of inter-related clans, governed by a council of elders and a hereditary chief. Social life is organized by a complex web of kinship relations and obligations. At the time of the study, there were no local markets, electricity, cars or public utilities in these villages, whose populations vary from 100 to 250 people.

(a) *Are Fijian food taboos an adaptation to marine toxins?*

Given this population's substantial reliance on marine resources, we suspected that ciguatera fish poisoning might be a significant health threat. Ciguatera poisoning is the most common form of fish poisoning and afflicts populations dependent on marine resources throughout the tropics [27]. Ciguatera toxins are produced by a marine dinoflagellate associated with macroalgae and accumulate up the food chain, most commonly achieving dangerous levels in large, often predatory, fishes [28]. Symptoms include neurological (e.g. paraesthesia) and physical (e.g. diarrhoea) effects, which can be severe and endure for months [29]. Occasionally, poisoning can be fatal. Most notably, for our purposes, research also indicates that ciguatera toxins can harm foetuses [30] and can pass to infants through breast milk [31].

We used a battery of interview instruments to (i) assess the extent of fish poisoning, (ii) capture the distribution of local taboos during pregnancy and breastfeeding, and (iii) estimate the impact of these taboos on rates of fish poisoning. To assess fish poisoning, we gathered data from a random sample of 60 adults across our three villages, asking about illnesses that occurred after consuming foods from the sea (see the electronic supplementary material). To study food taboos during pregnancy and breastfeeding, our team conducted a tripartite interview series with all women in our study villages who have given birth to at least one child. As part of this, we used a checklist of 17 food items that was designed to include both a range of toxic marine species based on the scientific literature [32] and a diverse sampling from across the local diet. To represent the most toxic fish species, we included moray eels (*dabea*), barracuda (*silasila*) and rock cod (*batisai*). For moderately toxic species, we added sea turtles (*vonu*) and sharks (*iko*). While sea turtle poisonings (chelonitoxication) have been recorded, very little is known about these toxins and their chemical structures have not been identified. Similarly, sharks are associated with both ciguatera poisoning and elasmobranch poisoning, though it remains unclear whether these are different. Most members of these fish categories carry only subclinical levels of poison, and all of the items on our checklist are regularly caught and consumed by most villagers. In fact, many of these species are important food sources (see the electronic supplementary material), with both turtles and moray eels being prized foods. We also included porcupine fish, freshwater eels and octopi, to examine the potential impact of certain cognitive biases.[3] To avoid missing any food categories with our checklist, we also had women free list tabooed foods for pregnancy and breastfeeding before doing our checklists.

Our final step in assessing these taboos as an adaptation was to examine whether they do indeed reduce the incidence of fish poisoning during pregnancy and breastfeeding. Ideally, we would examine a sample of women containing both those who report adhering to the fish taboos and those who do not; or, at least compare those who are close to the adaptive repertoire (which is also the consensus set of taboos) against those who are not. However, as shown below, we find a very high degree of consensus on tabooing the most dangerous species, so there is not much variation to work with. Instead, based on recall data from two detailed reproductive history interviews with 75 women in three villages (269 pregnancies), we calculated the rates of getting fish poisoning during five different life periods: (i) pregnancy, (ii) the last 28 weeks of pregnancy, (iii) breastfeeding, (iv) pregnancy and breastfeeding together, and (v) all of adult life when a woman is neither pregnant nor breastfeeding. Comparing the rates for periods (i)–(iv) against (v), we can assess whether these taboos are operating effectively. Note, we are calculating the rate for the last 28 weeks of pregnancy (ii) because our research also shows that during pregnancy sickness (*kune ca*), which occurs during the first trimester, a substantial percentage of village women avoid all fishes (finding their smell disgusting), but this is limited only to the first trimester.

(i) *Results and discussion of fish poisoning and taboo distribution*

Our interviews on fish poisoning (*ika gaga*) show that symptom profiles correspond closely with clinical diagnoses reported in the medical literature for Oceania, and firmly establish that ciguatera poisoning is a prevalent local problem. Overall, 58 per cent (CI 95: 45–71%) of adults reported at least one episode of poisoning. On average, acute symptoms lasted a week and chronic symptoms endured for about a month. For those who had at least one episode, the average number of episodes was 2.1 (see the electronic supplementary material).

Drawing on our interviews about food taboos during pregnancy and breastfeeding, figure 1 displays the frequencies of taboo reports for each of the food categories on our checklist.[4] During pregnancy, *only* the toxic species are reported as tabooed by the vast majority of women (over 87%), which we labelled the 'consensus grouping'. An 'intermediate grouping' of food avoidances with reported frequencies ranging from about 13 to 37 per cent includes octopi, porcupine fish, freshwater eels, meat (from land animals) and spices. The 'no-avoidance grouping' includes seven items that were reported as avoidances by less than 5 per cent of women, including staple categories of fruits, yams and cassava.

During breastfeeding, the taboo patterns are similar to pregnancy save for two differences. First, the frequencies of reported taboos drop across 12 of the 17 food categories, including dramatic drops for sharks and sea turtles, with sharks but not sea turtles tabooed by a slim majority. This difference between pregnancy and breastfeeding taboos may arise for a couple of reasons (admittedly *post hoc*), consistent with our cultural evolutionary interpretation. It may be that marine toxins pose less danger to infants, since they are further along in development or because the potency of the toxin declines as it passes through the mothers' body and into the breast milk. Or, it may be that the increased caloric demands of lactation [33,34], vis-à-vis gestation, shift to reduce the optimal set of taboos. In our population, the

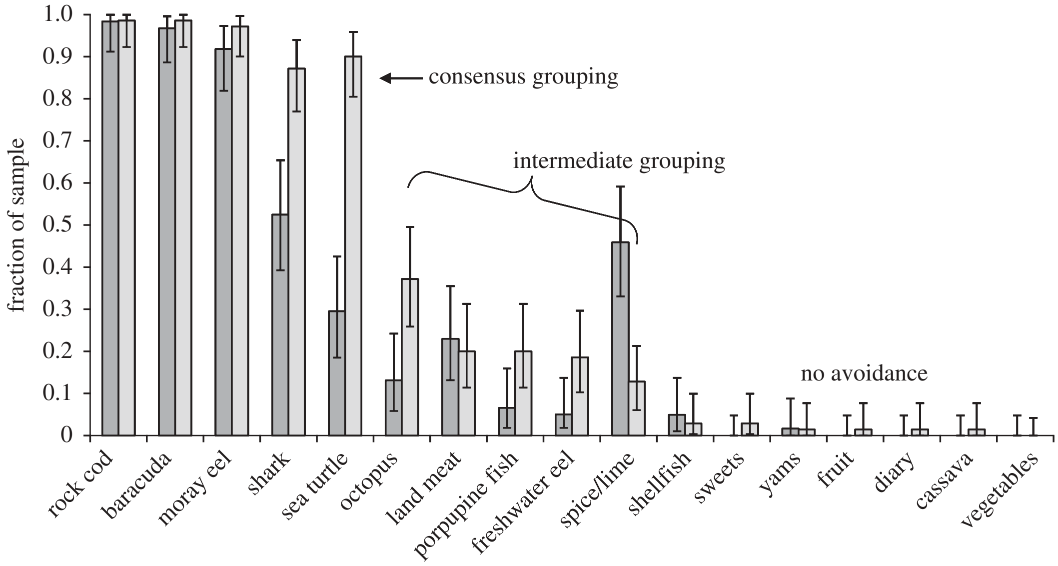

Figure 1. Taboos reported by women for 17 types of food during pregnancy ($n = 70$) and breastfeeding ($n = 61$). The error bars are 95% exact confidence intervals. Dark grey bars, breastfeeding; light grey bars, pregnancy.

effect of this increase in caloric demands can be observed in the substantial increases in reports of cravings during lactation versus pregnancy across all our food categories (see the electronic supplementary material). Given the higher caloric demands during breastfeeding and the relatively lower toxicity of sharks and turtles, women who drop these taboos during lactation may increase their overall health and success (family size), thus increasing their likelihood of being learned from.

Second, reports of taboos on spices increased substantially during breastfeeding. Some Fijian women reported that eating spices causes gastrointestinal discomfort in nursing infants. This is consistent with some Western medical recommendations, although opinion varies [35]. A few women also explicitly reported that they avoid spices during pregnancy in preparation for breastfeeding, so as not to cause discomfort to their newborns. This may explain both the non-trivial frequency of reported spice taboos during pregnancy and the increase in spice taboos during breastfeeding.

Analyses of our free lists of taboos, which asked women to list tabooed foods for pregnancy and breastfeeding before doing our checklists, confirm the above patterns for the toxic species in our checklist, and show that red snapper, a known-to-be highly toxic species [36], is also tabooed by the vast majority of village women. A few other rarely encountered larger species may also be important here. These data make clear that the vast majority of fish species are *not* tabooed during pregnancy and lactation.[5] Findings from the free lists are in the electronic supplementary material.

Ethnographic evidence indicates that these taboos may be old, stable and widespread. In the early 1930s in the Southern Lau, at the opposite end of the Fijian archipelago, Thompson reports pregnancy taboos using the identical Fijian words we now hear in Yasawa (*ika tava*, roughly, 'fish that must be sliced'), and specifically cites sea turtles and moray eels [37]. Currently, in Yasawa, the phrase *ika tava* (or *ika tavatava*) would add sharks and the aforementioned larger species to the list of Lauan taboos. The correspondence is important,

Table 1. Comparison of mean rates of fish poisoning in women for five life periods. n.a., not applicable.

number	relevant periods	mean rate (poisoning per year)	Wilcoxon signed-rank p-value
(i)	during pregnancy	0.043	0.0008
(ii)	during the final 28 weeks of pregnancy	0.048	0.0011
(iii)	during breastfeeding	0.027	0.0001
(iv)	during pregnancy and breastfeeding	0.033	0.0005
(v)	adulthood not including pregnancy or breastfeeding	0.070	n.a.

given the separation in time and space, as it suggests these taboos are widespread and temporally stable (see electronic supplementary material).

To address the question of whether these taboos have any real impact, table 1 shows the rate of getting fish poisoning during five key life periods. Period (v) captures all of adulthood for women except for (not including) periods of pregnancy (mean 2.7 years) and breastfeeding (mean 4.7 years). The chances of getting fish poisoning in any given year of this period is 7 per cent. During pregnancy and the final 28 weeks of pregnancy, the rates are 4.3 and 4.7 per cent, respectively. The rate increases for the last 28 weeks, as we would expect, because women with pregnancy sickness avoid fish during their first trimester. This is noteworthy since women are more susceptible to toxins during pregnancy than during other periods [38]. During breastfeeding, the rate is the lowest at 2.7 per cent, which is consistent with an improvement in a woman's resistance to toxins after pregnancy, and a continuing adherence to the major taboos.

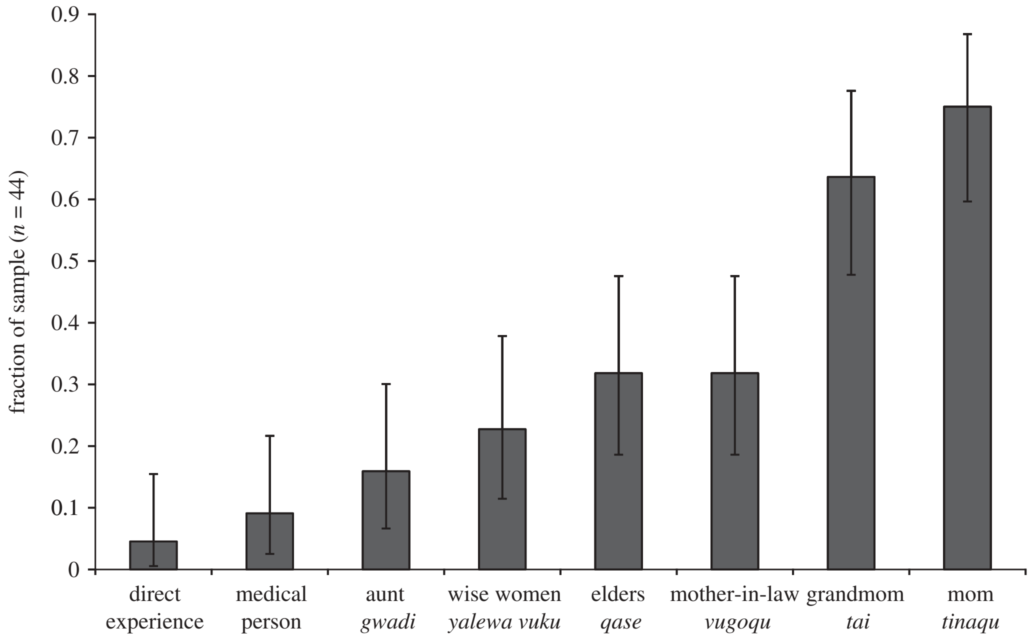

Figure 2. Distribution of reports about how women learned their food taboos. Error bars are 95% exact confidence intervals.

The breastfeeding rate is less than half the rate experienced by women when not observing the taboos. Because these data are highly non-normally distributed, table 1 provides a non-parametric test to assess the likelihood that the means for the two distributions are the same. The distribution for each of the first four periods is tested against period (v). These *p*-values indicate that the mean rates of fish poisoning for periods (i) to (iv) are significantly below the rate for the rest of adulthood (period v).

It is important to acknowledge that these findings on fish poisoning rates, which are consistent with our argument, do not decisively show that the taboos themselves reduce rates of marine intoxication. Women may be influenced by other forces during pregnancy and breastfeeding that lower their rates, besides the taboos. Note, however, that particularly during breastfeeding, women report craving fish (see the electronic supplementary material), and need to consume substantially more calories. Yet, they experience lower rates of marine intoxication. Taken in light of what is known about both the dangerous species tabooed and the susceptibility of pregnant women to toxins, such evidence takes a step towards establishing these taboos as a cultural adaptation.

Our results so far indicate that widely shared taboos during pregnancy and lactation target toxic marine species. When caloric demands rise during breastfeeding, the least toxic species drop from the set of consensus taboos. Non-toxic food sources were never observed among the consensus set of taboos. Pregnant and breastfeeding women, who all report observing the vast majority of the consensus taboos, experience lower rates of fish poisoning than those same women during the rest of their adult lives.

(b) *An adaptive repertoire built by selective cultural learning?*

To examine the mechanisms sustaining this adaptive pattern, we first asked a sample of women *how* they acquired their food taboos (note, we did not ask from *whom* they learned). Following the analysis of these data, we further traced the transmission network of *yalewa vuku* (wise women), who were identified as an important source of food taboos. We asked every person over age 7 in two neighbouring villages who they consider to be a *yalewa vuku*. Additionally, data on perceived knowledge were gathered in a separate interview (performed during a prior field season) by asking everyone over age 6 to list those who know the most about medicinal plants (traditional medicine and local remedies). See the electronic supplementary material for details.

(i) *Results and discussion of selective cultural learning*

Participants' responses to the question of how they acquired their food taboos were categorized as shown in figure 2 (some gave two responses). The results indicate two important features of these taboos. First, our results suggest that these are principally culturally transmitted, and not acquired by direct experience nor evoked by environmental circumstances. Less than 5 per cent of women mentioned learning anything from direct experience or observation, and *all* those people who mentioned direct experience also mentioned learning from other people (see the electronic supplementary material).

Second, the patterns of transmission are consistent with the model-based learning mechanisms described above, when the evolving system is near equilibrium. Figure 2 shows that most women learned from their mothers, grandmothers or mothers-in-law, as these models are generally low cost, accessible and share fitness incentives with the learner. However, almost a quarter of women reported learning from *yalewa vuku* (wise women) and almost a third reported learning from *qase* (elders, generally referring to senior non-close-relatives). *Yalewa vuku* are women who are well respected and considered knowledgeable about traditional medicine, birthing and child care, as well as other skills traditionally considered the province of women. It is a recognized, though

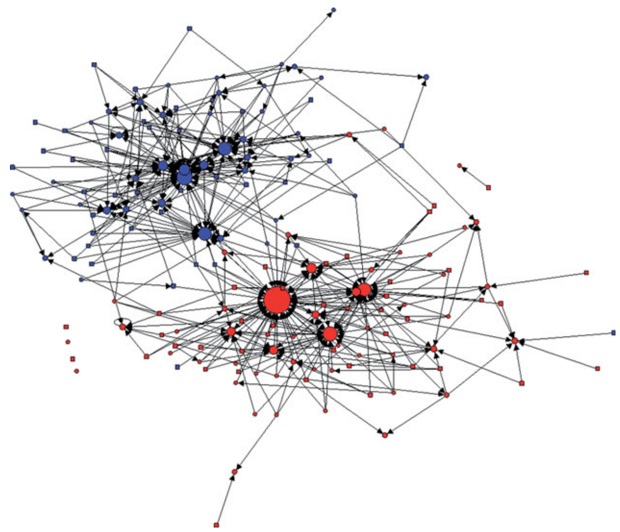

Figure 3. Network for *yalewa vuku*. The nodes represent villagers, with the circles indicating females and the squares males. Each arrow points from the person interviewed to one of the individuals named. The colours of the nodes distinguish the two villages. The size of the node is proportional to its indegree centrality, which is the total of individuals who selected the node as a *yalewa vuku*.

informal and emergent, social role. By selectively attending to such preferred models, learners can improve on cultural variants acquired from their family members. Modelling efforts suggest that, over generations, this tendency can stabilize a population at an adaptive equilibrium [5].[6]

To study the pathways of transmission from *yalewa vuku*, we asked people to name the *yalewa vuku*. Each respondent spontaneously named between zero and five people. The network in figure 3 illustrates that there is substantial agreement on who the *yalewa vuku* are (i.e. the network is centralized) and that a handful of individuals have a disproportionate impact on cultural evolution. Only 61 individuals were nominated (111 were never nominated). Of these, only 25 people received more than five nominations and only three received more than 25. One person received 60 nominations, nearly twice as many as the second ranked person (see the electronic supplementary material). This consensus on who is a *yalewa vuku* indicates that substantial differences in prestige exist among women in this regard.

Building on the link established above between the transmission of taboos and *yalewa vuku*, we tested our hypothesis that learners will use cues of age and of perceived expert knowledge to select from whom to learn by regressing the indegree for all women on their ages and their perceived knowledge of medicinal plants. Indegree is the number of nominations each woman received as a *yalewa vuku*. Since the dependent variable is bounded at its mode, zero, we used a generalized linear model with a negative binomial link function. In addition to age and perceived knowledge, we included each woman's formal education (varying from 0 to 12 years) to control for any effects this might have on *yalewa vuku* status. Table 2 shows that all three variables reveal substantial predictive effects on being selected as a *yalewa vuku* (see the electronic supplementary material).

Table 2. Regression analysis using age and plant knowledge to predict indegree of *yalewa vuku*.

variable	coefficient	*p*-value
age (years)	0.066	7.2E−13
knowledge (noms)	0.052	0.001
education (years)	0.2	0.002

While broadly consistent with the evolutionary predictions discussed above, these empirical patterns are not consistent with alternative cultural evolutionary models that assume (i) purely individual learning [39], (ii) all parental or unbiased transmission [40], or (iii) some combination of parental transmission and individual learning—*guided variation* [3]. These models are not consistent because selective learning biases, which are not part of these models, appear to be an important mechanism in sustaining the adaptive patterns we observed. More complex models that permit vertical or familial transmission combined with selective cultural learning, individual learning and natural selection acting on cultural variation could also consistent with our findings [41] (see the electronic supplementary material).

These data support the theory that (i) the consensus taboos have evolved to protect women and their offspring from marine toxins and (ii) that these cultural processes are driven at least partly by cultural learning mechanisms, shaped by natural selection, that focus learners' attention on those individuals most likely to possess fitness-enhancing cultural traits (in this case, prestigious, knowledgeable older women).

(c) *Non-adaptive by-products of cognitive processes?*

While most mothers agreed on which species were definitely tabooed (the potentially toxic species), the intermediate group in figure 1 suggests that there is a tendency towards false positives—that is, reporting something as tabooed that 'ought' not be tabooed (and could safely be eaten). Our approach also provides some potential insights into why certain foods, especially land meat, freshwater eels and octopi, were tabooed by a non-trivial minority of the population.

(i) *Why animal foods but not plant foods?*

During at least the later portions of human evolutionary history, our ancestors probably relied on (i) animal foods as sources of protein, fat and other nutrients and (ii) vast bodies of culturally transmitted knowledge about plants and animals [42]. This implies that our psychological machinery for culturally acquiring eating preferences and practices ought to be influenced by error-managing biases aimed at meat, and particularly at mammalian meat, given its tendency vis-à-vis other foods to carry parasites and pathogens dangerous to humans. Such a learning bias would favour the adoption of practices that help avoid pathogens and parasites. As a by-product, such a bias will tend to create positive frequencies of meat avoidances, and sometimes spread such avoidances to consensus [43]. Given this, it is not surprising that—except for spices—the most avoided foods on our checklists (and free lists) are *all* animal foods. Even shellfish maintained frequencies significantly different from zero during both pregnancy and breastfeeding.

Consistent with this, meat from the only local mammalian food sources (pigs and cows) was reported as tabooed by about one-fifth of the sample during both pregnancy and breastfeeding. Our initial work on Fijian folkbiology indicates that these land mammals are considered more similar to humans than any other animal foods typically eaten. Interestingly, everyone recorded as having a taboo in this meat category noted that it applied to pigs (*vuaka*). Only one person cited anything else, in addition to pigs (cows, *bulmakau*). Taboos on pigs re-emerge across many cultural contexts and some speculate alternatively that pigs (i) are particularly targeted because they consume garbage, faeces, etc. (while cows, e.g. eat grasses [43]) or (ii) bear some similarity to humans. By contrast, in the craving data mentioned above, everyone who reported craving meat cited beef as preferred [44] (discussed in the electronic supplementary material).

(ii) *Why freshwater eels?*

Our species' reliance on accumulated bodies of information about plants and animals appears to have shaped our cognition in adaptive ways that foster the organization and inferential extension of such information [45]. Two aspects of this folkbiological cognition are relevant here. The first aspect, category-based induction, permits inferences from knowledge about a single instance to be extended more broadly [46]. For example, when one learns something about one particular lion (it climbs trees), she can, with decreasing degrees of confidence, extend it to all members of a subspecies, to the species and beyond. The second aspect, taxonomic inheritance, permits learners to infer a substantial number of characteristics about a folkspecies by learning or inferring in which higher level category it resides [47,48]. For example, merely by finding out that a robin is a type of bird, one can infer that robins bleed, lay eggs and have hollow bones (details in the electronic supplementary material).

Using category-based induction, we suspect some of our sample—lacking decisive *culturally transmitted* input regarding freshwater eels (which are not toxic)—may have projected from the strong taboos on moray eels to freshwater eels. Put another way, if two people you trust tell you opposite things regarding the taboos on freshwater eels, you may be more inclined to accept that freshwater eels are tabooed if you (i) already believe morays are taboo and (ii) perceive morays and freshwater eels as similar. The electronic supplementary material presents a parallel argument for inductions from puffers to porcupine fish.

With (i) moray eels established as a taboo above, we sought to explore (ii) by examining whether adults in these villages perceive freshwater eels (*duna*) as similar to moray eels (*dabea*) vis-à-vis eight other folkspecies (seven marine folkspecies and humans). The seven marine folkspecies are sea turtles (*vonu*), lobsters (*moci*), porcupine fish (*sokisoki*), puffer fish (*vocivocia*), shark (*iko*), barracuda (*silasila*) and surgeonfish (*balagi*). Using perceived similarity measures collected from 55 randomly selected adults, we performed a hierarchical clustering analysis. These findings (see the electronic supplementary material) confirm that our participants do indeed perceive moray eels as substantially more similar to freshwater eels than to any of the other nine folkspecies. Our analysis also shows a high degree of consensus on the relative similarities of these folkspecies. This sets the stage for category-based induction to operate as hypothesized.

To test this hypothesis, we constructed an analysis based on the following logic: learners who—owing to their position in the networks of cultural transmission, their own learning skill or their life history—received weak or ambiguous culturally transmitted information about freshwater eels, thus permitting a stronger reliance on category-based induction, are also likely to have received ambiguous information on other items in the checklist. Consequently, we compared the vectors of checklist responses across all food categories (except freshwater eels) with the consensus response (modal answers) for those reporting taboos on freshwater eels against those who did not. If our proposal is correct, those who reported freshwater eel avoidances should have a lower mean agreement with the consensus response than those who did not. Supporting our hypothesis, the mean agreement for those citing freshwater eels as taboo was 87 per cent while those who did not showed a mean agreement of 93 per cent (one-tailed t-test, $p = 0.016$).

(iii) *Why octopus?*

For octopus, we hypothesize that the meat-avoidance bias combines with a salience possessed by organisms that are not readily identified as members of higher level categories in local folkbiological taxonomies [49,50]. In common parlance, these categorically ambiguous animals would seem weird compared with other living kinds. Cognitively, this salience may be adaptive on average because our folkbiological cognition relies on taxonomic inheritance from higher level categories (like bird, fish or mammal) to supply individuals with a wide range of information about generic animal kinds (like robin or trout); consequently, animals that cannot be identified with a higher level category do not deliver the benefit of taxonomic inheritance. Lacking taxonomically inherited information, animal kinds may be mysteriously or suspiciously salient compared with other animal kinds. Combining this mysteriousness with the fitness impacts of eating something toxic or approaching something deadly, learners may be biased to avoid categorically ambiguous kinds.

To establish whether *sulua* (squid and octopi) are actually more categorically ambiguous than other folkspecies on our checklist, we asked 140 adults in three villages to state whether each of 17 folkspecies is a kind of (i) *ika* (glossed as fish), (ii) *manumanu* (non-fish, non-shellfish, animal), (iii) *vivili* (roughly, shellfish), and (iv) *vatu* (stone). For each of these four higher level categories, we went through the entire list of folkspecies before moving to the next higher level category, so answers were not forced to be mutually exclusive (i.e. people could have said that sharks are both an *ika* and a *manumanu*, but they did not). Figure 4 shows that *iko* (sharks), *batisia* (rock cod) and *dabea* (moray eels) are

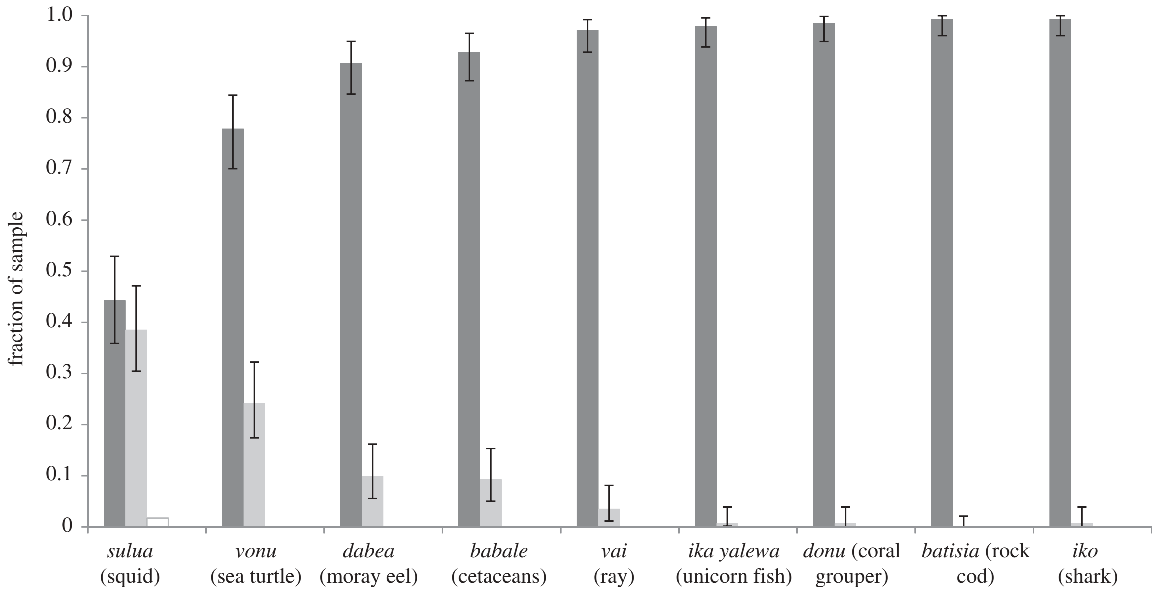

Figure 4. Higher level categorization for eight folkspecies. Error bars are 95% exact CI ($n = 140$). Black bars, *ika*; light grey bars, *manumanu*; white bars, *vivili*; dark grey bars, *vatu*.

unambiguously *ika* (fish), with over 90 per cent citing them as *ika* (thus, these taboos cannot be explained by categorical ambiguity). *Vonu* (sea turtle) shows some categorical ambiguity, with only 79 per cent citing it as an *ika*, and the rest putting it as a *manumanu*. The categorization of turtles as a 'fish' is common throughout Oceania [51]. *Sulua* (squid and octopus), however, emerged as totally ambiguous, with 44 per cent saying they are a kind of *ika* (of which sharks and groupers are near-perfect exemplars) and 39 per cent going for *manumanu* (15% of people said they did not know which category to choose). *Sulua* are a categorically ambiguous animal that cannot be readily identified with a higher level category. This may make them easy to taboo.

4. CONCLUSION

Broadly, these findings demonstrate how, by applying evolutionary theory to understanding our cognitive processes for cultural learning and considering their population-level consequences, we can explain the patterns observed in culturally evolved distributions of beliefs and practices. More specifically, these finding support theoretical work showing how evolved biases in human cultural learning can give rise to adaptive behavioural patterns and how evolved psychological adaptations, such as folkbiological cognition, influence or bias cultural patterns, sometimes in locally non-adaptive ways. This approach effectively incorporates 'cultural explanations' under the larger umbrella of evolutionary theory without ignoring our species' heavy reliance on sophisticated forms of social learning.

This research was approved by the Behavioural Research Ethics Board at the University of British Columbia, and by the Internal Review Board at Emory University.

This research was funded by the National Science Foundation grant BCS-0239683. We thank the people of Teci, Dalomo and Bukama, as well as our Fijian research team, including Samisoni Nanovu, Joape Kuruyawa and Naomi Tuberi. We'd also like to thank Peter Richerson, Richard McElreath and Mark Lubell for helpful comments on earlier drafts.

ENDNOTES

[1]To intuitively grasp this, realize that at equilibrium most parents have the adaptive repertoire (of food avoidances, for example). If children acquire the practices or beliefs of their parents, they will not (on average) update from others outside the family, since (i) everyone else is mostly doing the same thing as the parents and (ii) anyone who is not doing the same thing as their parents (at equilibrium) is doing, on average, worse.
[2]This is a cultural analogue to the balance between selection, drift and mutation in genetic models. Such theoretical findings do not depend on assumptions about the discreteness of cultural traits or on high-fidelity transmission [52].
[3]Note that parts of the porcupine fish can be extremely toxic. However, when prepared with skill, the porcupine fish is safe to eat. This distinguishes these fish from the other toxic species described.
[4]No differences were found among the villages in taboos except for octopus, see the electronic supplementary material.
[5]As part of these same investigations, we also gathered data on foods that disgusted women during their first trimester. These findings support existing theories of food aversions during pregnancy as an adaptation [38], but there was no connection between the foods that women reported aversions towards (disgust) during their first trimester (which are not tabooed) and the taboos that extend throughout pregnancy and breastfeeding. Thus, there is little reason to suspect that these cultural prohibitions represent an extension of experiences during pregnancy sickness, though this may be important elsewhere [44].
[6]This requires that learners' subjective evaluations actually tend to pick out women who have acquired more adaptive ideas, beliefs, values and knowledge.

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