Darwinian Gastronomy: Why We Use Spices

Spices taste good because they are good for us

Paul W. Sherman and Jennifer Billing

Spices are plant products used in flavoring foods and beverages. For thousands of years, aromatic plant materials have been used in food preparation and preservation, as well as for embalming, in areas where the plants are native, such as Hindustan and the Spice Islands (Govindarajan 1985, Dillon and Board 1994). During and after the Middle Ages, seafarers such as Marco Polo, Ferdinand Magellan, and Christopher Columbus undertook hazardous voyages to establish routes to trading ports in primary spice-growing regions (Parry 1953). The spice trade was so crucial to national economies that rulers repeatedly mounted costly expeditions to raid spice-growing countries, and struggles for the control of these countries precipitated several wars. When Alarich, a leader of the Goths, laid siege to Rome in AD 408, he demanded as ransom various precious metals and 3000 pounds of pepper (Scheiper 1993).

Today, spice use is ubiquitous, but spices are far more important in some cuisines than others. Most people have experienced this variability firsthand, when traveling in foreign lands, dining at international restaurants, or preparing exotic recipes at home. Japanese dishes are often "delicate," Indonesian and Szechwan dishes "hot," and middle European and Scandinavian dishes "bland." Usually these differences are merely chalked up to cultural idiosyncrasies. Several years ago, we became curious about this interpretation. We wondered if there are any predictable patterns of spice use and, if so, what factors might underlie them. In this article, we summarize the results of our inquiries. We found that spice use is decidedly nonrandom and that spices have several beneficial effects, the most important of which may be reducing foodborne illnesses and food poisoning.

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Humans have borrowed plants' chemical "recipes" for evolutionary survival for use in cuisine to combat foodborne microorganisms and to reduce food poisoning

What is a spice?

"Spice" is a culinary term, not a botanical category—it does not refer to a specific kind of plant or plant part (Farrell 1990). Indeed, spices come from various woody shrubs and vines, trees, aromatic lichens, and the roots, flowers, seeds, and fruits of herbaceous plants (Figure 1). Cookbooks generally distinguish between seasonings (spices used in food preparation) and condiments (spices added after food is served), but not between herbs and spices. However, herbs, which are defined botanically (as plants that do not develop woody, persistent tissue), usually are called for in their fresh state, whereas spices generally are dried (Figure 2). Salt is sometimes thought of as a spice, but it is a mineral.

Each spice has a unique aroma and flavor, which derive from compounds known as phytochemicals or "secondary compounds" (because they are secondary to the plant's basic metabolism). These chemicals evolved in plants to protect them against herbivorous insects and vertebrates, fungi, pathogens, and parasites (Fraenkel 1959, Walker 1994). Most spices contain dozens of secondary compounds. These are plants' recipes for survival—legacies of their coevolutionary races against biotic enemies.

Patterns of spice use

Conventional wisdom tells us that cuisines of tropical countries are spicier than those of northern countries, but patterns of spice use around the world have not been quantified. To do so, we located "traditional" cookbooks, which were written primarily to archive the author's native cuisine. We analyzed recipes in 93 traditional cookbooks from 36 countries (at least two books from each country) and quantified the use of 43

Table 1. Mean annual temperature, number of meat-based recipes analyzed (in 93 cookbooks), mean number of spices per recipe, and the four most frequently used spices (i.e., used in the highest proportion of recipes) for each of the 36 countries included in this study.

Country[a]	Mean annual temperature (°C)	Recipes analyzed	Spices per recipe	Frequently used spices[b]
Thailand	27.6	118	4.6	Garlic, onion, chilis[c], pepper[d]
Philippines	27.0	118	3.0	Pepper, onion, garlic, lemon/lime
India	26.9	91	9.3	Ginger, onion, chilis, coriander
Malaysia	26.9	60	5.4	Onion, garlic, chilis, ginger
Indonesia	26.8	120	6.9	Garlic, onion, chilis, coriander
Nigeria	26.5	82	2.6	Chilis, onion, pepper, nutmeg
Ghana	25.9	95	2.2	Onion, pepper, chilis, ginger
Vietnam	24.6	84	4.5	Pepper, garlic, onion, chilis
Brazil	23.9	132	4.2	Onion, pepper, parsley, garlic
Mexico	23.1	123	4.4	Onion, garlic, chilis, pepper
Kenya	22.1	73	5.4	Garlic, onion, pepper, chilis
Ethiopia	21.1	56	7.5	Onion, garlic, chilis, ginger
Lebanon	20.6	98	4.7	Pepper, onion, cinnamon, garlic
Israel	19.1	145	3.9	Pepper, onion, garlic, lemon/lime
Australia	18.6	64	3.4	Pepper, onion, parsley, lemon/lime
Morocco	18.3	104	5.8	Onion, pepper, parsley, saffron
South Africa	17.2	108	2.6	Pepper, onion, lemon/lime, chilis
Greece	16.7	118	4.4	Pepper, onion, garlic, lemon/lime
Iran	16.7	85	5.0	Onion, pepper, lemon/lime, turmeric
Portugal	15.0	84	4.5	Pepper, garlic, parsley, onion
Japan	14.3	103	2.1	Onion, lemon/lime, ginger, chilis
Italy	14.0	86	3.4	Pepper, garlic, parsley, lemon/lime
Korea	12.1	81	3.5	Garlic, onion, pepper, sesame
France	12.1	216	3.8	Pepper, onion, garlic, parsley
Hungary	10.3	80	3.0	Onion, pepper, paprika, parsley
Ireland	9.6	90	3.2	Pepper, onion, garlic, parsley
England	8.8	223	2.1	Pepper, onion, lemon/lime, parsley
Germany	8.8	169	3.2	Onion, pepper, lemon/lime, parsley
Austria	8.8	188	2.7	Onion, pepper, parsley, lemon/lime
Denmark	8.3	87	1.9	Pepper, onion, bay leaf, parsley
Poland	7.8	141	0.3	Onion, pepper, bay leaf, parsley
Sweden	5.4	134	2.5	Pepper, onion, allspice, parsley
Finland	3.0	62	2.1	Pepper, onion, mustard, lemon/lime
Norway	2.8	77	1.6	Pepper, parsley, onion, lemon/lime
United States				
Northern	8.6	284	5.4	Pepper, onion, garlic, parsley
Southern	17.8	248	5.0	Onion, chilis, pepper, parsley
China				
Northeast	13.4	187	2.3	Onion, ginger, pepper, garlic
Southwest	19.4	243	3.2	Ginger, onion, pepper, garlic

[a]Countries are listed in order of mean annual temperature, except for the United States and China. We divided those two countries into two regions that we analyzed separately.
[b]In order of use.
[c]Chilis are capsaicin-containing peppers.
[d]Pepper refers to black and white pepper.

spices in these countries (Table 1).

In gathering our data, we did not distinguish between seasonings and condiments or between herbs and spices. We focused on meat-based recipes (those in which at least one-third of the volume or weight consisted of meat) rather than vegetable-based recipes for two reasons. First, traditional cookbooks have many more meat-based dishes than vegetarian dishes, enabling us to obtain adequate sample sizes (Table 1). Second, unrefrigerated meats spoil faster than vegetables and are more often associated with foodborne disease outbreaks (Sockett 1995). Thus, any relationship between spoilage and spice use should be more apparent in meat-based than vegetable-based recipes.

In summarizing the data, we encountered two problems. The first was whether or not to treat onions (*Allium cepa*: chives, leeks, and shallots) and chilis (*Capsicum frutescens*: capsaicin-containing peppers) as spices. Although these plants are often used solely as spices, they are also served as main dishes. Following the lead of previous authors (e.g., Farrell 1990, Tainter and Grenis 1993, Hirasa and Takemasa 1998), we decided to include both plants as spices because, regardless of the quantities called for, they always contribute their phytochemicals to the cuisine. The second problem was how to treat the comparative information statistically, because not all countries are equally "independent" (e.g., due to shared ancestry or recent immigration). However, because it is unclear how to assess independence of a specific cultural practice, such as spice use, and because our sample was so broad (representing every continent and 16 of the world's 19 major linguistic groups [Ruhlen 1987]), we treated all countries as if they were independent and used nonparametric analyses.

We tabulated the ingredients in 4578 meat-based recipes and discovered that most of them (93%) call for at least one spice. On average, recipes called for 3.9 ± 1.7 (SD) spices, although some lacked spices entirely and others had up to 12 spices. In 10 countries—Ethiopia, Kenya, Greece, India, Indonesia, Iran, Malaysia, Morocco, Nigeria, and Thailand—every meat-based recipe we examined called for at least one spice, whereas in Scandinavian countries one-third of the recipes did not call for any spices.

The frequency of use of individual spices also varied widely (Figure 3). Black pepper and onion were called for most frequently, in 63% and 65% of all meat-based recipes, respectively. Other commonly used spices included garlic (35% of recipes), chilis (24%), lemon and lime juice (23%), parsley (22%), ginger (16%), and bay leaf (13%). However, the majority of spices were used infrequently. Of the 43 spices we analyzed, 35 (81%) were used in less than 10% of the recipes, and 29 (67%) were used in less than 5% of the recipes.

Figure 1. Spices are plant parts. They come from woody shrubs and vines, trees, aromatic lichens, and the roots, flowers, seeds, and fruits of herbaceous plants. Photo: Thomas Neuhaus, Neuhaus Features.

Antimicrobial properties of spices

Why are spices used? The obvious answer is that they enhance food flavor, color, and palatability. Of course this is true as far as it goes. However, such a proximate (immediate cause) explanation does not address the ultimate (evolutionary) questions of why cuisines that contain pungent plant products appeal to people and why some phytochemicals are tastier than others. Answers to proximate and ultimate questions are complementary, not mutually exclusive, and full understanding requires explanations at both "levels of analysis" (Sherman 1988).

A clue to the ultimate reason for spice use may lie in the protective effects of phytochemicals against plants' biotic enemies. After all, meat and other food items are also attacked by bacteria and fungi, indeed by some of the same species that afflict plants. Throughout recorded history, foodborne bacteria (especially species of *Clostridium*, *Escherichia*, *Listeria*, *Salmonella*, *Shigella*, and *Vibrio*) or their toxins have been serious health concerns, and they still are (Hui et al. 1994, WHO 1996). If spices were to kill such microorganisms or inhibit their growth before they could produce toxins, use of spices might reduce foodborne illnesses and food poisoning (Billing and Sherman 1998). If this antimicrobial hypothesis were true, several predictions should be fulfilled.

Prediction 1. Spices should exhibit antibacterial and antifungal activity. Microbiologists and food-product developers have conducted laboratory experiments that involve challenging numerous foodborne bacteria, fungi, and yeasts with phytochemicals extracted from spice plants. Multiple techniques have been used to investigate inhibition, and the primary data vary considerably in quality and quantity for different spices. Nevertheless, it is now clear that many spices have potent antimicrobial properties (e.g., Hargreaves et al. 1975, Shelef 1984, Deans and Ritchie 1987, Zaika 1988, Beuchat 1994, Nakatani 1994, Hirasa and Takemasa 1998).

We were particularly interested in the ability of spices to inhibit bacteria because bacteria are more commonly incriminated in foodborne disease outbreaks than yeasts or fungi (Varnam and Evans 1991, Todd 1994). All 30 spices for which we located laboratory test results were found at some concentration to kill or inhibit at least 25% of the bacterial species on which they had been tested, and 15 of these spices inhibited at least 75% of bacterial species (Figure 4). Garlic, onion, allspice, and oregano were found to be the most potent spices: They inhibited or killed every bacterium they were tested on. Most of the tested microor-

Figure 2. The spice trade flourishes today, as it has for thousands of years. Here, ground spices are displayed at Carmel Souk, an open-air market in Tel Aviv. Photo: Eliot M. Herman.

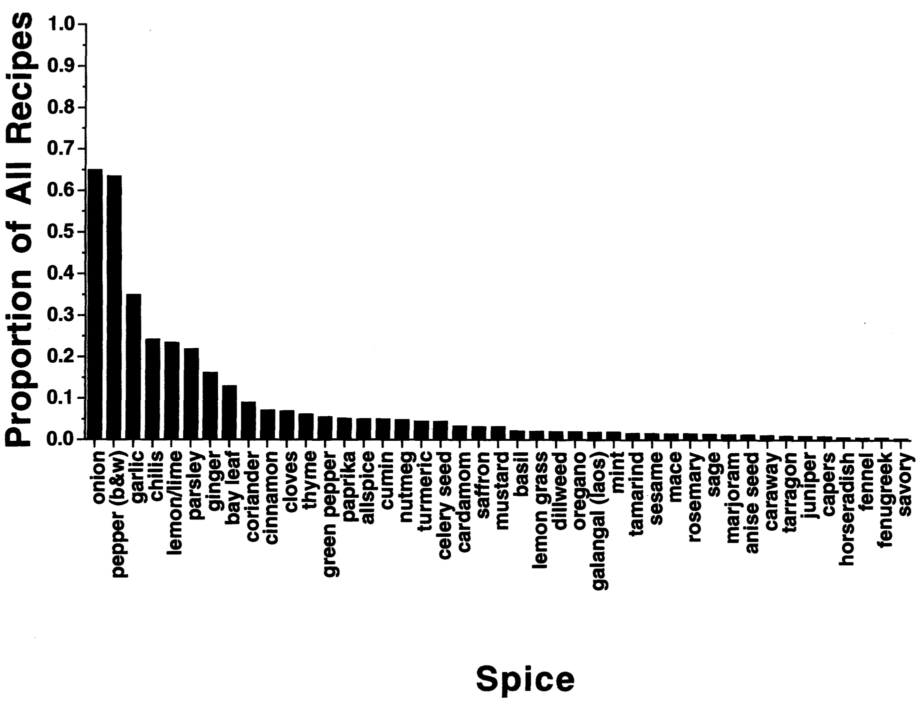


Figure 3. Proportions of 4578 meat-based recipes that called for each of 43 spices. The recipes we surveyed came from 93 traditional cookbooks from 36 countries worldwide. Each country was represented by at least two cookbooks. Modifed from Billing and Sherman (1998).

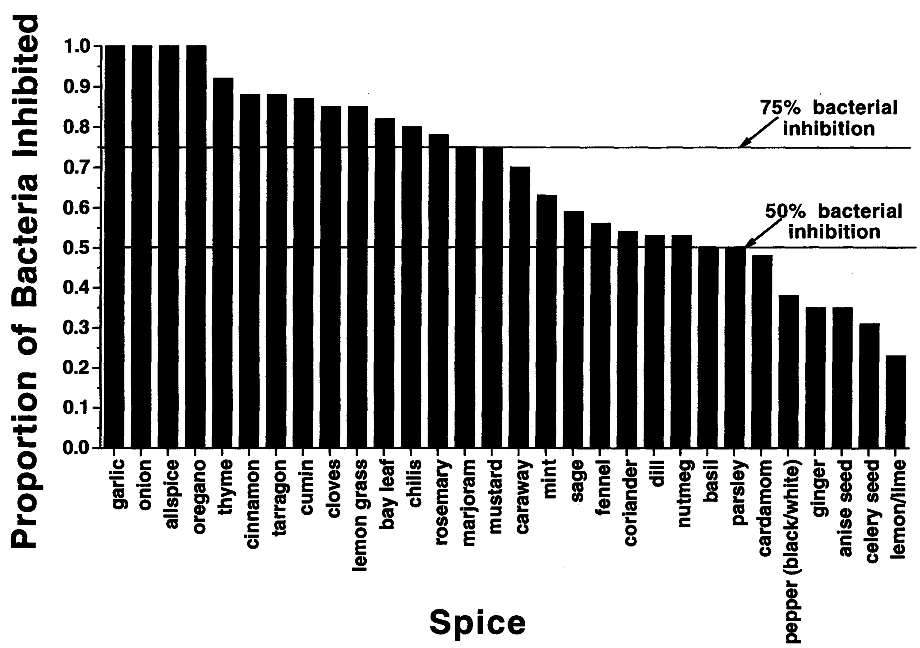


Figure 4. Antimicrobial properties (i.e., killing or growth inhibition) of 30 spices. The spices are arrayed from greatest to least inhibition. Each bar indicates the fraction of all food-spoilage bacterial species on which the spice or its phytochemicals have been tested (at any concentration) in the laboratory that were killed or whose growth was inhibited. (The number of bacterial species on which each spice was tested ranged from 4 to 31.) All 30 spices inhibited or killed some tested bacterial species; 15 spices inhibited or killed at least 75% of the species, and 4 spices (garlic, onion, allspice, and oregano) inhibited or killed all of the tested species. Modifed from Billing and Sherman (1998).

ganisms are widely distributed geographically, so they have the potential to contaminate foods everywhere.

Prediction 2. Use of spices should be greatest in hot climates, where unrefrigerated foods spoil especially quickly. Uncooked meats and meat dishes that are prepared in advance and stored at room temperatures for more than a few hours typically build up massive bacterial populations, especially in tropical climates (Hobbs and Roberts 1993). Therefore, we used each country's average annual temperature as a relative indicator of its rate of meat spoilage. Our test assumes that traditional meat-based recipes were developed before widespread refrigeration. We cannot directly evaluate this assumption because the cookbooks we examined rarely discussed the history of individual dishes. However, the assumption seems reasonable because any recipe that has been around for more than five generations (approximately 100 years) would pre-date electrical refrigeration. Most of the recipes we examined probably were at least that old.

We used climate atlases (e.g., Bair 1992) to tabulate information on mean temperatures in all 36 countries (Table 1). Temperatures ranged from 2.8 °C (Norway) to 27.6 °C (Thailand). Consistent with the prediction, we found that as average temperatures increased among countries, there were significant increases in the fraction of recipes that called for at least one spice, the mean numbers of spices per recipe, and the numbers of different spices used (Figure 5). For example, India's cuisine included 25 different spices, of which an average of 9.3 were called for per recipe, whereas Norwegian cuisine included only 10 different spices and called for an average of 1.6 per recipe. In Hungary, which has a temperate climate, the cuisine included 21 spices, of which an average of 3.0 were called for per recipe.

The relative use of many individual spices also varied with climate. Among countries, as average temperature increased, so did the frequency of use of chilis, garlic, and onion (Figures 6 and 7), as well as that of anise, cinnamon, coriander, cumin, ginger, lemongrass, turmeric, basil, bay leaf, cardamom, celery, cloves, green peppers, mint, nutmeg, saffron, and oregano (see also Hirasa and Takemasa 1998). The first 10 of these spices are "highly inhibitory" (at least 75% of tested bacterial species inhibited; see Figure 4), and the positive relationships were statistically significant. There were negative relationships between temperature and frequencies of use for 10 other spices, but they were significant only for dill and parsley, neither of which has potent antimicrobial activity.

Prediction 3. A greater proportion of bacteria should be inhibited by recipes from hot climates than from cool climates. In support of this prediction, as average annual temperatures increased among countries, the mean fraction of recipes that called for each one of the highly inhibitory spices used in those countries increased significantly (Figure 8a). However, this correlation did not hold for less inhibitory spices (Figure 8b). There was also a positive relationship between the fraction of bacterial species inhibited by each spice and the fraction of countries that used that spice, indicating widespread use of the spices that are most effective against bacteria.

To further test this corollary, we tried to determine if spices used in each country are particularly effective against local bacteria. Unfortunately, however, no comprehensive lists of indigenous bacteria are available for any country in our sample. To estimate inhibition, therefore, we chose 30 meat-based recipes at random from the cookbooks for each country and tallied how many of 30 "target" bacterial species would be inhibited or killed by at least one spice in each recipe. The target bacteria were those that have been challenged experimentally with the greatest number of spices, including such widespread species as *Aeromonas hydrophila*, *Bacillus cereus*, *Bacillus subtilus*, *Clostridium botulinum*, *Listeria monocytogenes*, *Escherichia coli*, *Salmonella pullorum*, *Staphylococcus aureus*, and *Streptococcus faecalis*. Results of this analysis (Figure 9) showed that as annual temperatures increased, the estimated fraction of food spoilage bacteria inhibited by the spices in each country's recipes increased significantly. Therefore, the cuisine of hotter countries potentially has greater antibacterial activity.

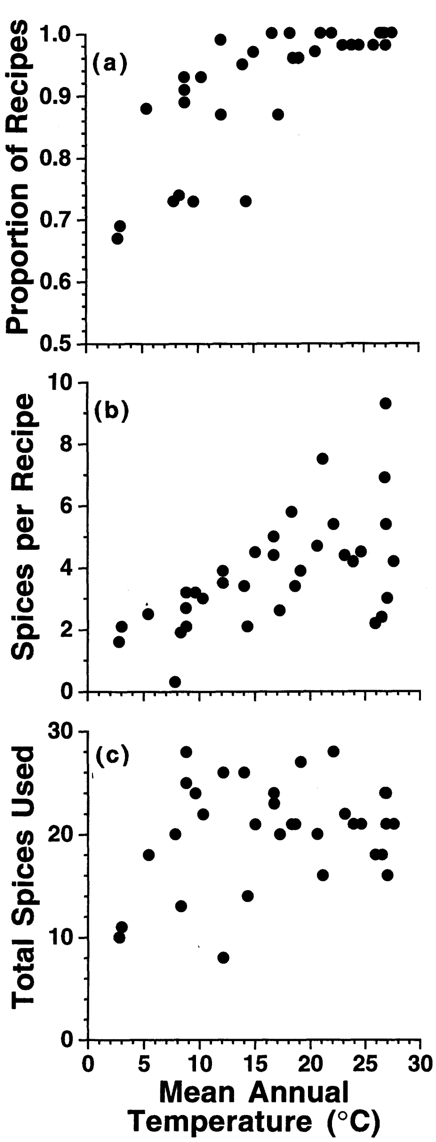


Figure 5. Relationships between mean annual temperature and spice use for the 34 nonregional countries we analyzed (i.e., excluding the United States and China). (**a**) Relationship between mean annual temperature and the proportion of meat-based recipes calling for at least one spice (r = 0.740, df = 32, $P < 0.001$). (**b**) Relationship between mean annual temperature and the mean numbers of spices called for per recipe (r = 0.572, df = 32, P = 0.002). (**c**) Relationship between mean annual temperature and the total number of spices used in the country (r = 0.216, df = 32, P = 0.286). Modifed from Billing and Sherman (1998).

Prediction 4. Within a country, cuisine from high latitudes and elevations (i.e., cooler climates) should contain fewer and less potent spices than cuisine from lower latitudes and elevations. We located regional cookbooks for only two countries, China and the United States. Consistent with the prediction, in both countries the total number of spices used, the fraction of recipes that called for at least one spice, and the frequency of use of highly inhibitory spices were greater in southern regions than in northern regions. The mean number of spices per recipe was greater in southern China than in northern China, but no such difference was evident in the United States (Table 1). In both countries, the spices called for in an average southern recipe had significantly greater antibacterial potential than those in northern recipes, mirroring the among-country pattern (Billing and Sherman 1998). Because altitude-specific cookbooks are rare, we were unable to evaluate how altitude affects spice use.

Prediction 5. Quantities of spices called for in recipes should be sufficient to produce antimicrobial effects, and cooking should not destroy the potency of phytochemicals. The primary literature in food microbiology that we surveyed usually reported the minimum concentrations of purified phytochemicals that were necessary to inhibit growth of foodborne bacteria in vitro. Typically, these were solutions containing 0.5–4.0% purified spice chemicals (i.e., 30–2000 μg/ml), which is within the range of spice concentrations used in cooking (Shelef 1984, Giese 1994, Hirasa and Takemasa 1998). However, there are as yet no analyses of how different amounts and types of spices affect microorganisms in cuisine. Evaluating the antimicrobial efficacy of various spices in vivo (i.e., restaurants and homes) would be a fascinating (and potentially lucrative) project.

Regarding the effects of cooking, most phytochemicals are thermostable, although a few are destroyed by heat (Moyler 1994). Some spices (e.g., garlic, pepper, rosemary, and onion) are typically added at the beginning of cooking, whereas oth-

Figure 6. Garlic (Liliaceae: *Allium sativum*; top), onion (*Allium cepa*; top), and chilis (Solanaceae: *Capsicum frutescens*; bottom) grow in all countries we sampled and have powerful antimicrobial effects. Photos: Thomas Neuhaus, Neuhaus Features.

ers (e.g., parsley and cilantro [i.e., coriander leaf]) are added near the end (Figure 10). According to cookbook authors, the "delicate" flavors of the latter would be destroyed by heat. If, as seems likely, thermostable spices are the ones added early and thermolabile spices are added later (or are used primarily as condiments), differences in timing of use may function to maintain beneficial antimicrobial properties (and corresponding flavors) until food is served.

Spice synergism

Pepper and lemon (and lime) juice are among the most frequently used spices (Figure 3), but they are unusual in that the frequency with which they are used does not change much across the temperature gradient (Figure 11). Moreover, they are among the least effective bacteriocides (Figure 4). Do these patterns weaken the antimicrobial hypothesis, or do these two spices function in a different way than "typical" spices?

We believe that the second explanation is correct, and we suggest that pepper and citric acid play special roles—that is, as synergists. Citric acid potentiates the antibacterial effects of other spices because low pH disrupts bacterial cell membranes (Booth and Kroll 1989). Foods to which lemon or lime juice are added require less heating to cause the same levels of bacterial mortality that take place in foods cooked at higher pH and temperature for a longer time. Black pepper comes from *Piper nigrum*, an exclusively tropical plant that has several useful properties. For example, the compound piperine inhibits the ubiquitous, deadly bacterium *Clostridium botulinum* (Nakatani 1994). Black pepper is also a "bioavailability enhancer," meaning that it acts synergistically to increase the rate at which cells, including microorganisms, absorb phytotoxins (Johri and Zutshi 1992).

Many other spices exhibit greater antibacterial potency when they are mixed than when used alone (Ziauddin et al. 1996). Some are combined so frequently that the blends have acquired special names. An intriguing example is the French "quatre epices" (pepper, cloves, ginger, and nutmeg), which is often used to make sausages. Sausages (*botulus* in Latin) are a rich medium for bacterial growth and have frequently been implicated as the source of botulinum toxin. Other blends, such as curry powder (which contains 22 different spices), pickling spice (15 spices), and chili powder (10 spices), are broad-spectrum antimicrobial melanges.

Other uses of spices

In addition to their uses in cooking, individual spices and blends are employed as coloring agents, antivirals (including suppressing HIV), brain stimulants, and aphrodisiacs (Hirasa and Takemasa 1998). Among traditional societies, many spice plants also have ethnopharmacological uses, often as topical or ingested antibacterials and vermicides (Chevallier 1996, Cichewicz and Thorpe 1996). A few spices, particularly garlic, ginger, cinnamon, and chilis, have for centuries been used to counteract a broad spectrum of ailments, including dysentery, kidney stones, arthritis, and high blood pressure (Johns 1990, Duke 1994).

However, the use of spices in food preparation differs from medicinal use in three ways. In cooking, spices are used without regard to diners' health status, they are used in tiny quantities, and they are routinely added to specific recipes. This pattern suggests that the "targets" of spice chemicals are on or in the food before it is ingested. By contrast, in medicinal usage, spices are taken in response to particular maladies, in large quantities, and not with any particular dish—more like swallowing a pill than preparing a meal.

An interesting question is whether other animals also "spice" foods. Presently, the answer appears to be "no." However, "vegetation" does form a small but significant fraction of the diet of most wild carnivores, including foxes, coyotes, and cougars (e.g., Parker 1995). Undoubtedly, much of this plant material serves as nutrition, for example, when meat is scarce.

Nevertheless, frequent ingestion of vegetation is potentially interesting in the context of the antimicrobial hypothesis because most wild carnivores scavenge carrion, so they are frequently exposed to food-spoilage bacteria and fungi. Moreover, some animals that store food add plants with antibacterial and antifungal properties to their caches (e.g., brown bears sometimes cover carcasses with *Spaghnum* moss [Elgmork 1982], and some stingless bees build honey pots by mixing plant resins with wax [Roubik 1983]). These possible prophylactic uses should not be confused with consumption of aromatic plants by wild primates as a potential means of "self-medication" (e.g., Huffman and Wrangham 1994).

Costs of spices

In light of the beneficial effects of spices, why aren't spices used equally often everywhere? The answer probably lies in the costs of spice use, including financial costs to procure parts of plants that do not grow locally (e.g., consider the price of Spanish saffron), illnesses caused by ingesting spices that are themselves contaminated (e.g., with bacteria, fungi, or animal feces), and other hazards of ingesting too many plant secondary compounds and essential oils. Indeed, Ames et al. (1990) and Beier and Nigg (1994) reviewed evidence that phytochemicals in many common spices have mutagenic, teratogenic, carcinogenic, or allergenic properties. As one example, in small quantities chilis have antimicrobial and therapeutic effects, but ingestion of large amounts of capsaicin has been associated with necrosis, ulceration, and carcinogenesis (Surh and Lee 1996). The implication is that too much of a good thing can be bad. In hot climates, benefits of avoiding foodborne illnesses and food poisoning apparently outweigh the various costs of spices. But in cool climates, where unrefrigerated foods decay more slowly, benefits of further retarding spoilage may not be worth the costs and risks.

Even in countries where spices are heavily used, pre-adolescent children (Rozin 1980) and women in their first trimester of pregnancy (Profet 1992) typically avoid highly spiced foods, especially meats. These differences in spice use may have a similar adaptive basis. For example, Profet (1992) suggested that morning sickness may function to reduce maternal intake of foods containing teratogens during the early phase of embryogenesis, when delicate fetal tissues are most susceptible to chemical disruption. Indeed, women who experience morning sickness are less likely to miscarry than women who do not (Weigel and Weigel 1989). Young children, who are growing rapidly, may also be particularly sensitive to environmental mutagens. Once pregnancy has progressed into the second trimester and once children reach puberty, the dangers of food poisoning and foodborne illnesses may again outweigh the mutagenic risks associated with phytochemicals (Flaxman and Sherman in press). Interestingly, maternal ingestion of spices late in pregnancy or during lactation can slightly bias offspring toward accepting spices (e.g., Altbacker et al. 1995).

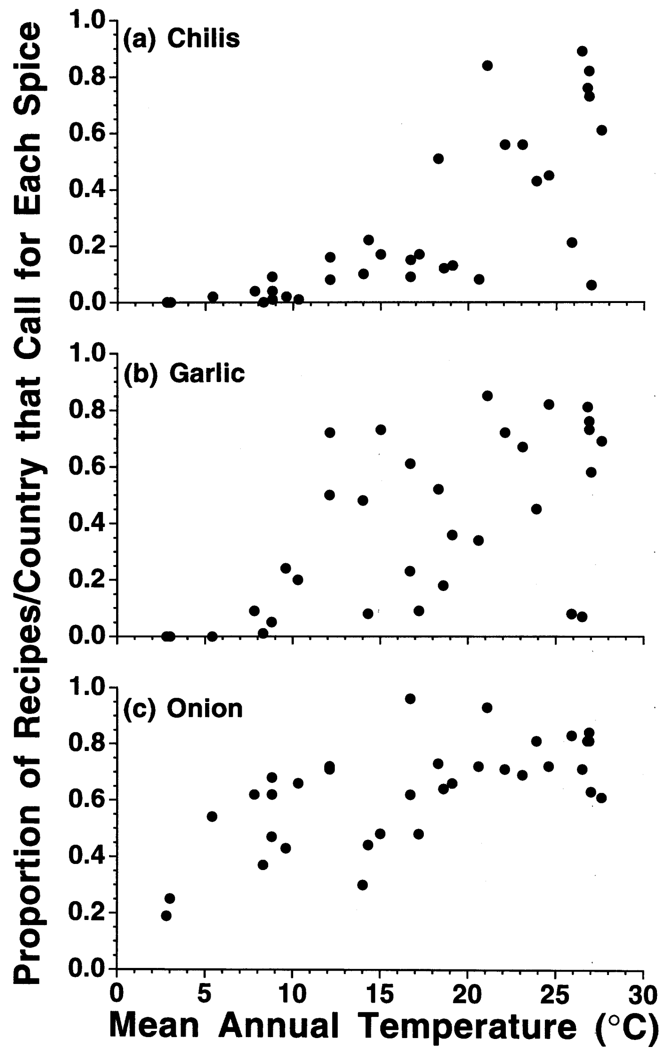


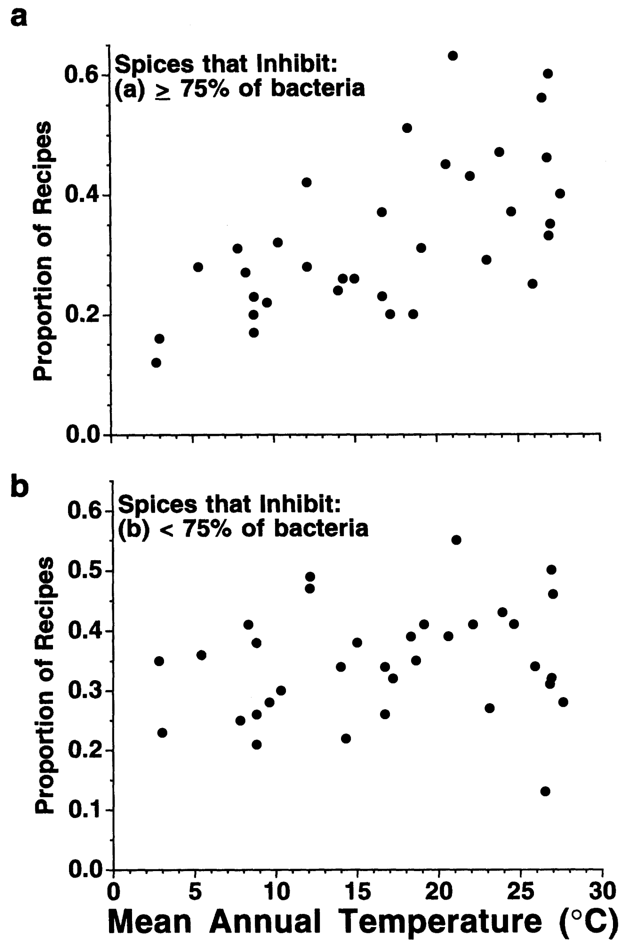
Figure 7. Relationships between each nonregional country's mean annual temperature and the proportion of its meat-based recipes that call for one of three highly inhibitory spices (at least 75% bacterial inhibition; see Figure 3). (**a**) Chilis (capsaicin-containing peppers; $r = 0.757$, $df = 32$, $P < 0.001$). (**b**) Garlic ($r = 0.635$, $df = 32$, $P < 0.001$). (**c**) Onion ($r = 0.652$, $df = 32$, $P < 0.001$). Modifed from Billing and Sherman (1998).

Alternative hypotheses to explain spice use

The antimicrobial hypothesis is not the only explanation that has been proposed to explain spice use; however, careful consideration of the alternatives reveals that all have significant flaws. For example, one proximate hypothesis is that spices disguise the smell and taste of spoiled foods (Govindarajan 1985). Our finding that traditional meat-based recipes from hotter countries more frequently called for spices, and more pungent spices, is consistent with this idea because there would more often be foul smells and bad tastes to "cover up" due to rapid spoilage. However, the problem with this hypothesis as an ultimate (evolutionary) explanation is that it ignores the potentially serious negative consequences of ingesting foods laced with bacteria or their toxins. Even poorly nourished individuals would often be better off if they recognized and passed up foods containing potentially deadly spoilage microorganisms.

A second proximate alternative to explain spice use is that spicy foods

Figure 8. Relationships between each nonregional country's mean annual temperature and the proportion of meat-based recipes that call for spices that inhibit at least 75% of bacteria (**a**; $r = 0.668$, $df = 31$, $P < 0.001$) or less than 75% of bacteria (**b**; $r = 0.248$, $df = 31$, $P > 0.10$). Modifed from Billing and Sherman (1998).



are preferred in hot climates because they increase perspiration and help cool the body evaporatively. However, although chilis and horseradish can cause sweating in some people, most spices do not have this effect (Rozin and Schiller 1980). Thus, evaporative cooling cannot be a general explanation for the increased spice use in hot climates. Moreover, physiological mechanisms of temperature regulation obviously operate to keep us cool without the necessity of finding, eating, and dealing with the potentially negative side effects of phytochemicals.

One alternative ultimate hypothesis for spice use is that wherever spices are difficult to obtain and are therefore expensive, individuals signal their wealth and social status (e.g., to rivals or potential mates) by using them lavishly. This hypothesis would apply primarily to spice plants with restricted ranges (e.g., pepper, allspice, fenugreek, nutmeg, and cinnamon). However, it does not predict or explain the multiple positive correlations between temperature and spice use we found for spices that are available ubiquitously (e.g., Figure 7). Also, this hypothesis is difficult to reconcile with the fact that the rarest spices tend to be used most commonly in the tropics, because it is in these locations where the plants are endemic and, presumably, therefore, least expensive.

A second alternative ultimate hypothesis is that spices supply chemicals that, in small quantities, have beneficial effects other than inhibiting food spoilage microorganisms. For example, certain phytochemicals, especially those found in garlic and onions, can aid digestion, modulate energy metabolism, and even help postpone some degenerative diseases, such as diabetes and cancer (Johns and Chapman 1995). Some other phytochemicals, particularly those in cloves, rosemary, sage, pepper, and mace, are powerful antioxidants (Lin 1994, Hirasa and Takemasa 1998). By retarding the oxidation of oil or fat, phytochemicals help preserve foods and also reduce the production of free radicals, which have been linked to cancer and aging. These effects are undeniably important, but they probably do not represent the primary reason for spice use because not all spices have these beneficial properties. Moreover, the need for micronutrients or antioxidants does not predict or explain the use of spices in recipes or the multiple positive correlations between temperature and spice use shown in Figures 5, 7, 8, and 9).

Finally, it is also possible that spice use may not confer any benefits. Under this hypothesis, patterns of spice use arise because people just take advantage of whatever aromatic plants are available to improve the taste of their food. Perhaps the phytochemicals in spices happen to resemble those found in sought-after foods, such as fat and sugar (Rozin and Vollmecke 1986), and as a result spices taste good. If this idea were correct, spice chemicals should be highly palatable, and spice-use patterns should correspond to local availability of spice plants.

However, neither prediction is fully supported. Although some spices are initially appealing (e.g., cinnamon, basil, and thyme), pungent spices, such as garlic, ginger, anise, and chilis, are distasteful to most people, especially children (Rozin 1980). Indeed, the capsaicin receptor is a heat-activated ion channel in the pain pathway (Caterina et al. 1997). For most unpalatable substances, an initial negative response is sufficient to maintain avoidance throughout life. However, preferences for spices develop during individuals' lifetimes, usually under familial guidance. Parents encourage

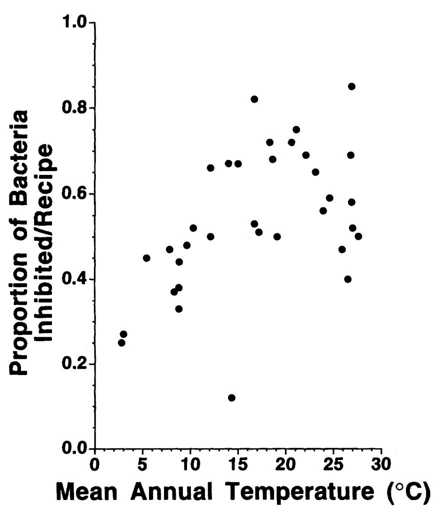


Figure 9. Relationship between the mean annual temperature of each nonregional country and the estimated fraction of 30 ubiquitous foodborne bacterial species that would be inhibited by the spices in the recipes of that country ($r = 0.516$, $df = 31$, $P < 0.001$). Modifed from Billing and Sherman (1998).

their children to use spices, and most children eventually come to like (or at least accept) them, implying that spice use is beneficial.

In addition, spices are not necessarily more available in hot climates than in cool ones. There is no relationship between the number of countries in which each spice plant grows (i.e., its native and domesticated range) and either the number of countries in which it is used or their annual temperatures (Billing and Sherman 1998). Because spices have been cultivated for thousands of years in the Old World (Zohary and Hopf 1994) and hundreds of years in the New World (Coe 1994), it seems likely that these patterns of spice plant availability reflect those that occurred when traditional recipes were developing.

Thus, correlations between spice use and annual temperature must be due to people in hot countries using a larger proportion of whatever spices are available locally (or importing more spices). Indeed, for 22 of 30 spices (73%), a larger percentage of recipes called for the spice in countries where the plant grows than where it does not grow; for 14 of the spices, these differences were significant ($P < 0.05$, Mann-Whitney tests). Of course, the spice trade (Figure 2) facilitates the use of nonindigenous spices. For example, onion and pepper are the two most frequently used spices in the world (Figure 3). *Allium* grows in all 36 countries we examined, but *Piper* grows in only 9 countries. Pepper is the world's most frequently traded spice (more than 90 million pounds per year are imported into the United States alone; Tainter and Grenis 1993). Thus, although local availability certainly influences spice use, use is not dictated solely by local availability.

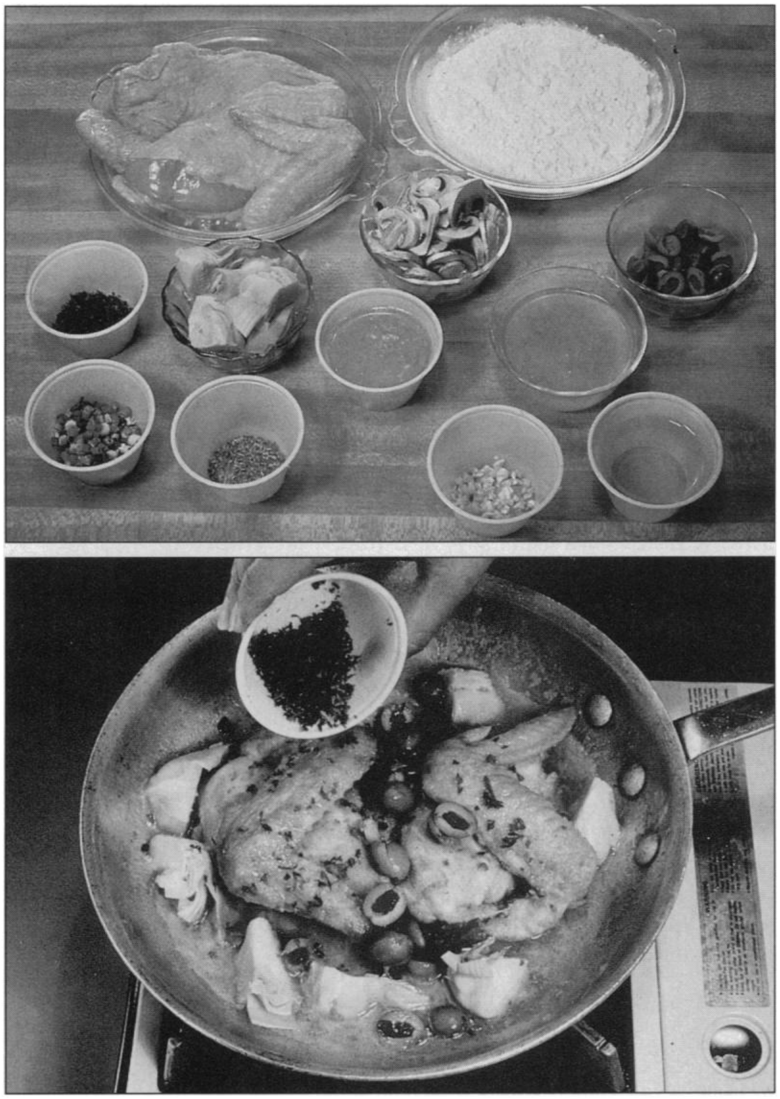


Figure 10. Some spices (e.g., garlic, pepper, rosemary, and shallots) are typically added at the beginning of cooking (top), whereas others (e.g., parsley and cilantro) are added near the end or are used as garnishes (bottom). These patterns in the timing of use may relate to differences in the thermal stability of different spices. Photos: Thomas Neuhaus, Neuhaus Features.

Origins of spice use

How did spice use begin? We hypothesize that people may have begun cooking with spices whose flavors were initially appealing or that made them feel good (due to digestive or vermicidal effects, among other things). As a result, spice-using families may also have been less likely to suffer from foodborne illnesses or food poisoning than families that did not use spices, especially in hot climates. Furthermore, spice-using families probably would have been able to store foods longer before they spoiled, enabling them to tolerate prolonged periods of food scarcity. Observation and imitation of the food-preparation habits of these healthier families by neighbors could have spread spice use rapidly through a society. Families that used appropriate spices would presumably rear more healthy offspring, who would then learn spice-use traditions from their parents. It even seems possible that people who lived in areas where certain spices were traditionally used might have developed physiologically heightened abilities to taste those phytochemicals. The possible existence of such intergroup variations in taste receptor sensitivity to spices are just beginning to be explored (Drewnowski and Rock 1995).

Eventually, however, new foodborne bacteria or fungi would immigrate, or indigenous microorganisms would evolve resistance to local spices. Individuals eating foods contaminated by these microbes would become ill. After humans, like many other creatures, eat something that makes them sick, they tend to avoid that taste (Milgram et al. 1977, Pelchat and Rozin 1982). The adaptive value of such "taste-aversion learning" is obvious (Rozin and Vollmecke 1986, Letarte et al. 1997). Adding a different spice to a food that caused such an illness might change its flavor enough to make it palatable again—because it tastes like a new food. At the same time, if the spice were to kill the microorganism(s) that caused the illness in the first place, then the food would again be rendered safe for consumption. As a result of this sequence of events, food aversions would more often be associated with unspiced (and unsafe) foods, whereas food likings would be associated with spicy dishes, especially in climates where foods spoil rapidly. Over time, the number of spices per recipe would proliferate due to iteration of this process—that is, sequential changes in taste, associated with inhibiting different bacteria and fungi.

Antimicrobial value of spices today

Despite the widespread availability of electrical refrigeration, antimicrobial properties of spices may still be useful. For example, there is an order-of-magnitude difference in the frequency of foodborne illnesses between modern Japan and Korea, nearby countries with similar temperate climates. During 1971–1990, food poisoning—primarily of bacterial origin—affected 29.2 out of every 100,000 Japanese but only 3.0 out of every 100,000 Koreans (Lee et al. 1996). Lee et al. (1996) suggested that the difference may have been due to cultural variations in food handling and preparation, and this explanation may well be correct. But, in addition, Korean meat-based recipes are spicier than those of Japan. Although meat-based recipes of Japan collectively used more kinds of spices (14) than those of Korea (8), Korean recipes more frequently called for at least one spice, contained more spices per recipe (Table 1), and more frequently called for highly inhibitory spices (Billing and Sherman 1998). As a result, an average Korean recipe most likely inhibits a significantly greater fraction of bacteria than an average Japanese recipe. One possible explanation for the fact that traditional Japanese recipes do not call for more spices is that they date from times when fresh seafood was continuously available from local waters. Today, more food is imported, and it comes from farther away. Traditional Japanese recipes may simply not include enough spices (antimicrobials) to cope with the pathogens in the imported food supply.

Of course, spice use is not the only way in which humans attempt to hold foodborne pathogens at bay. Meat products have traditionally been preserved by thoroughly cooking, smoking, drying, and salting them. Indeed, salt, which is available the world over, has been used for preservation for centuries (Multhauf 1996). And today, of course, the "front line" of defense against spoilage is refrigeration and freezing. We hypothesize that all these practices have been adopted for essentially the same reason: to minimize the impact of microorganisms that colonize our food.

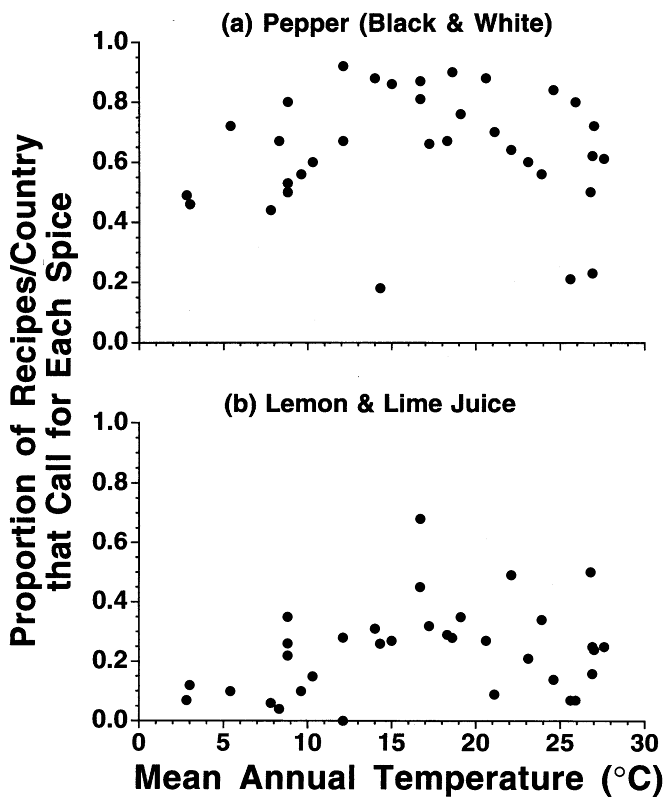


Figure 11. Relationships between each nonregional country's mean annual temperature and the proportion of that country's meat-based recipes that call for two spices (pepper or lemon or lime juice) that have low antimicrobial activity but that may potentiate the antimicrobial effects of other spices. (**a**) Black and white pepper ($r = 0.001$, df = 32, $P = 0.996$). (**b**) Lemon and lime juice ($r = 0.260$, df = 32, $P = 0.137$). Modifed from Billing and Sherman (1998).

Conclusion

Use of spices takes advantage of plant defensive compounds. Not surprisingly, in view of their evolved functions, these phytochemicals have antioxidant, antimicrobial, and antiviral properties. The use of spices essentially borrows plants' recipes for survival and puts them to similar use in cooking. Over time, recipes should "evolve" as new bacteria and fungi appear or indigenous species develop resistance to phytochemicals, requiring the addition of more spices or new spices to combat them effectively. However, there is a limit to how much of any one spice can be added before beneficial phytochemicals become phytotoxins. Thus, cookbooks from different eras are more than just curiosities. Essentially, they represent written records of our coevolutionary races against foodborne diseases. By cleansing foods of pathogens before consumption, spice users contribute to the health, longevity, and fitness of themselves, their families, and their guests. A Darwinian view of gastronomy thus helps us understand why "some like it hot" (spicy, that is!).

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References cited

Altbacker V, Hudson R, Bilko A. 1995. Rabbit-mothers' diet influences pups' later food choice. Ethology 99: 107–116.

Ames BN, Profet M, Gold LS. 1990. Dietary pesticides (99.99% all natural). Proceedings of the National Academy of Sciences of the United States of America 87: 7777–7781.

Bair FE, ed. 1992. The Weather Almanac. 6th ed. Detroit (MI): Gale Research.
Beier RC, Nigg HN. 1994. Toxicology of naturally occurring chemicals in food. Pages 1–186 in Hui YH, Gorham JR, Murrell KD, Cliver DO, eds. Foodborne Disease Handbook. Vol. 3: Diseases Caused by Hazardous Substances. New York: Marcel Dekker.
Beuchat LR. 1994. Antimicrobial properties of spices and their essential oils. Pages 167–179 in Dillon VM, Board RG, eds. Natural Antimicrobial Systems and Food Preservation. Wallingford (UK): CAB International.
Billing J, Sherman PW. 1998. Antimicrobial functions of spices: Why some like it hot. Quarterly Review of Biology 73: 3–49.
Booth IR, Kroll RG. 1989. The preservation of foods by low pH. Pages 119–160 in Gould GW, ed. Mechanisms of Action of Food Preservation Procedures. London: Elsevier.
Caterina MJ, Schumacher MA, Tominaga M, Rosen TA, Levine JD, Julius D. 1997. The capsaicin receptor: A heat-activated ion channel in the pain pathway. Nature 389: 816–824.
Chevallier A. 1996. The Encyclopedia of Medicinal Plants. New York: DK Publishing.
Cichewicz RH, Thorpe PA. 1996. The antimicrobial properties of chile peppers (*Capsicum* species) and their use in Mayan medicine. Journal of Ethnopharmacology 52: 61–70.
Coe SD. 1994. America's First Cuisines. Austin (TX): University of Texas Press.
Deans SG, Ritchie G. 1987. Antibacterial properties of plant essential oils. International Journal of Food Microbiology 5: 165–180.
Dillon VM, Board RG, eds. 1994. Natural Antimicrobial Systems and Food Preservation. Wallingford (UK): CAB International.
Drewnowski A, Rock CL. 1995. The influence of genetic taste markers on food acceptance. American Journal of Clinical Nutrition 62: 506–511.
Duke JA. 1994. Biologically active compounds in important spices. Pages 201–223 in Charalambous G, ed. Spices, Herbs, and Edible Fungi. Amsterdam: Elsevier.
Elgmork K. 1982. Caching behavior of brown bears (*Ursus arctos*). Journal of Mammalogy 63: 607–612.
Farrell KT. 1990. Spices, Condiments, and Seasonings. 2nd ed. New York: Van Nostrand Reinhold.
Flaxman SM, Sherman PW. In press. Morning sickness: A mechanism for protecting the embryo. Quarterly Review of Biology.
Fraenkel GS. 1959. The raison d'être of secondary plant substances. Science 129: 1466–1470.
Giese J. 1994. Spice and seasoning blends: A taste for all seasons. Food Technology 48: 87–90.
Govindarajan VS. 1985. Capsicum production, technology, chemistry, and quality. Part I: History, botany, cultivation, and primary processing. CRC Critical Reviews in Food Science and Nutrition 22: 109–176.
Hargreaves LL, Jarvis B, Rawlinson AP, Wood JM. 1975. The antimicrobial effects of spices, herbs and extracts from these and other food plants. Scientific and Technical Surveys, British Food Manufacturing Industries Research Association 88: 1–56.
Hirasa K, Takemasa M. 1998. Spice Science and Technology. New York: Marcel Dekker.
Hobbs BC, Roberts D. 1993. Food Poisoning and Food Hygiene. 6th ed. London: Edward Arnold.
Huffman MA, Wrangham RW. 1994. Diversity of medicinal plant use by chimpanzees in the wild. Pages 129–148 in Wrangham RW, McGrew WC, DeWaal FBM, Heltne PG, eds. Chimpanzee Cultures. Cambridge (MA): Harvard University Press.
Hui YH, Gorham JR, Murrell KD, Cliver DO, eds. 1994. Foodborne Disease Handbook. Vol. 1: Diseases Caused by Bacteria. New York: Marcel Dekker.
Johns T. 1990. With Bitter Herbs They Shall Eat It: Chemical Ecology and the Origins of Human Diet and Medicine. Tucson (AZ): University of Arizona Press.
Johns T, Chapman L. 1995. Phytochemicals ingested in traditional diets and medicines as modulators of energy metabolism. Recent Advances in Phytochemistry 29: 161–188.
Johri RK, Zutshi U. 1992. An Ayurvedic formulation "Trikatu" and its constituents. Journal of Ethnopharmacology 37: 85–91.
Lee W-C, Sakai T, Lee M-J, Hamakawa M, Lee S-M, Lee I-M. 1996. An epidemiological study of food poisoning in Korea and Japan. International Journal of Food Microbiology 29: 141–148.
Letarte A, Dube L, Troche V. 1997. Similarities and differences in affective and cognitive origins of food likings and dislikes. Appetite 28: 115–129.
Lin RI-S. 1994. Pharmacological properties and medicinal use of pepper (*Piper nigrum* L.). Pages 469–481 in Charalambous G, ed. Spices, Herbs, and Edible Fungi. Amsterdam: Elsevier.
Milgram NW, Krames L, Alloway TM. 1977. Food Aversion Learning. New York: Plenum Press.
Moyler DA. 1994. Spices—recent advances. Pages 1–71 in Charalambous G, ed. Spices, Herbs, and Edible Fungi. Amsterdam: Elsevier.
Multhauf RP. 1996. Neptune's Gift: A History of Common Salt. Baltimore: Johns Hopkins University Press.
Nakatani N. 1994. Antioxidative and antimicrobial constituents of herbs and spices. Pages 251–272 in Charalambous G, ed. Spices, Herbs, and Edible Fungi. Amsterdam: Elsevier.
Parker G. 1995. Eastern Coyote: The Story of Its Success. Halifax (Canada): Nimbus Publishing.
Parry JW. 1953. The Story of Spices. New York: Chemical Publishers.
Pelchat ML, Rozin P. 1982. The special role of nausea in the acquisition of food dislikes by humans. Appetite 3: 341–351.
Profet M. 1992. Pregnancy sickness as adaptation: A deterrent to maternal ingestion of teratogens. Pages 327–365 in Barkow J, Cosmides L, Tooby J, eds. The Adapted Mind. New York: Oxford University Press.
Roubik DW. 1983. Nest and colony characteristics of stingless bees from Panama (Hymenoptera: Apidae). Journal of the Kansas Entomological Society 56: 327–355.
Rozin P. 1980. Acquisition of food preferences and attitudes to food. International Journal of Obesity 4: 356–363.
Rozin P, Schiller D. 1980. The nature and acquisition of a preference for chili pepper by humans. Motivation and Emotion 4: 77–100.
Rozin P, Vollmecke TA. 1986. Food likes and dislikes. Annual Review of Nutrition 6: 433–456.
Ruhlen M. 1987. A Guide to the World's Languages. Vol. 1: Classification. Stanford (CA): Stanford University Press.
Scheiper R. 1993. Hot Spice. Contact 57. Springfield (NJ): Haarman and Reimer.
Shelef LA. 1984. Antimicrobial effects of spices. Journal of Food Safety 6: 29–44.
Sherman PW. 1988. The levels of analysis. Animal Behavior 36: 616–618.
Sockett PN. 1995. The epidemiology and costs of diseases of public health significance, in relation to meat and meat products. Journal of Food Safety 15: 91–112.
Surh Y-J, Lee SS. 1996. Capsaicin in hot chili pepper: Carcinogen, co-carcinogen, or anticarcinogen? Food and Chemical Toxicology 34: 313–316.
Tainter DR, Grenis AT. 1993. Spices and Seasonings. New York: VCH Publishers.
Todd ECD. 1994. Surveillance of foodborne disease. Pages 461–536 in Hui YH, Gorham JR, Murrell KD, Cliver DO, eds. Foodborne Disease Handbook. Vol. 1: Diseases Caused by Bacteria. New York: Marcel Dekker.
Varnam AH, Evans MG. 1991. Foodborne Pathogens. London: Mosby-Year Book.
Walker JRL. 1994. Antimicrobial compounds in food plants. Pages 181–204 in Dillon VM, Board RG, eds. Natural Antimicrobial Systems and Food Preservation. Wallingford (UK): CAB International.
Weigel RM, Weigel MM. 1989. Nausea and vomiting of early pregnancy and pregnancy outcome: A meta-analytical review. British Journal of Obstetrics and Gynaecology 96: 1312–1318.
[WHO] World Health Organization. World Health Report 1996. The State of World Health. Geneva: World Health Organization.
Zaika LL. 1988. Spices and herbs: their antimicrobial activity and its determination. Journal of Food Safety 9: 97–118.
Ziauddin KS, Rao HS, Fairoze N. 1996. Effect of organic acids and spices on quality and shelf-life of meats at ambient temperature. Journal of Food Science and Technology 33: 255–258.
Zohary D, Hopf M. 1994. Domestication of Plants in the Old World: The Origin and Spread of Cultivated Plants in West Asia, Europe, and the Nile Valley. 2nd ed. Oxford (UK): Oxford University Press.