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Overview article

Nature's chefs: Uniting the hidden diversity of food making and preparing species across the tree of life

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Abstract

There may be no such thing as a free meal, but many species have evolved mechanisms for other species to consume the literal fruits of their labors. In the present article, inspired by a chef's recognition that such species are "nature's chefs," we consider food-making species from the plant, animal, and fungal kingdoms, which produce food or mimic food to increase their own fitness. We identify three ways that species can produce or prepare meals—as food, drinks, or lures—and further distinguish between those providing an honest meal and those deceiving consumers with food mimics. By considering these species holistically, we highlight new hypotheses about the ecology and evolution of the widespread phenomenon of organisms that produce food for other organisms. We find surprising and useful generalities and exceptions among species as different as apple trees and anglerfish by examining species interactions across taxa, systems, and disciplines.

Keywords: drink, food, fruit, mimic, mutualism, nectar, nuptial gift, plating

Today, natural phenomena are often studied separately in different disciplines. Such is the case for the phenomenon in which organisms make, prepare, and offer food for other organisms. This recently became clear to us at a meeting called Talking Sense. The meeting brought together chefs, food scientists, neuroscientists, philosophers, ecologists, and evolutionary biologists. Some chefs were pleasantly surprised to learn that the fruits that they employ in their dishes evolved in plants, via natural selection, as a reward for animals to enhance their seed dispersal and, ultimately, their fitness (Levey et al. 2002, Schupp et al. 2010). "You mean to say," said one chef, "fruits are nature's chefs!" This simple utterance reflected a general sentiment among a number of the chefs and led to many consequent conversations about other contexts in which species in nature play, in varying forms, the role of the chef. Superficially, the insight of the human chefs at Talking Sense was that humans are united with many other organisms in making, preparing, and offering food to other individuals and that this connection had gone unnoticed because of the disciplinary split between the food industry and ecology. But further scrutiny revealed that the insight was actually broader. As we began to consult studies of species that make, prepare or offer food to other individuals, we found that not only was there no connection between the study of human chefs and, say, the study of the ways in which fruits have evolved to attract consumers (diners), there were also few connections between food-producing organisms across taxa and even habitats.

Our focus in the present article is on species that have evolved ways to produce or prepare food or drink items for consumers or diners or that deceive consumers by providing what are or appear to be food or drink so as to improve the fitness of their offspring and genes. In the present article, we use a holistic interdisciplinary approach to consider such species. We leverage the insights and approaches of our diverse fields; our team includes chef researchers, food scientists, a humanist, ecologists, and evolutionary biologists. In doing so, we highlight previously unnoticed mysteries (e.g., the dearth of fruits dispersed by predators), as well as the generalities and exceptions in the factors driving the evolution and ecology of food producers and consumers.

As we consider food-producing and -consuming organisms, we do so with an eye toward identifying connections between food making by nonhuman species and food preparation by chefs. We do this for several reasons. First, we note that there exist opportunities for individuals in the food industry, including chefs, to learn from and innovate in the context of a broader understanding of the evolution of food production by nonhuman species. With this potential in mind, we both identify opportunities for synergy and collaboration and attempt to avoid jargon that would make this work less legible to scholars and practitioners who are not evolutionary biologists. In addition, we also recognize that the work of chefs and other individuals in the food industry is ultimately embedded in the story of human evolution and the evolution of human food preparation, processing, and sharing. Food

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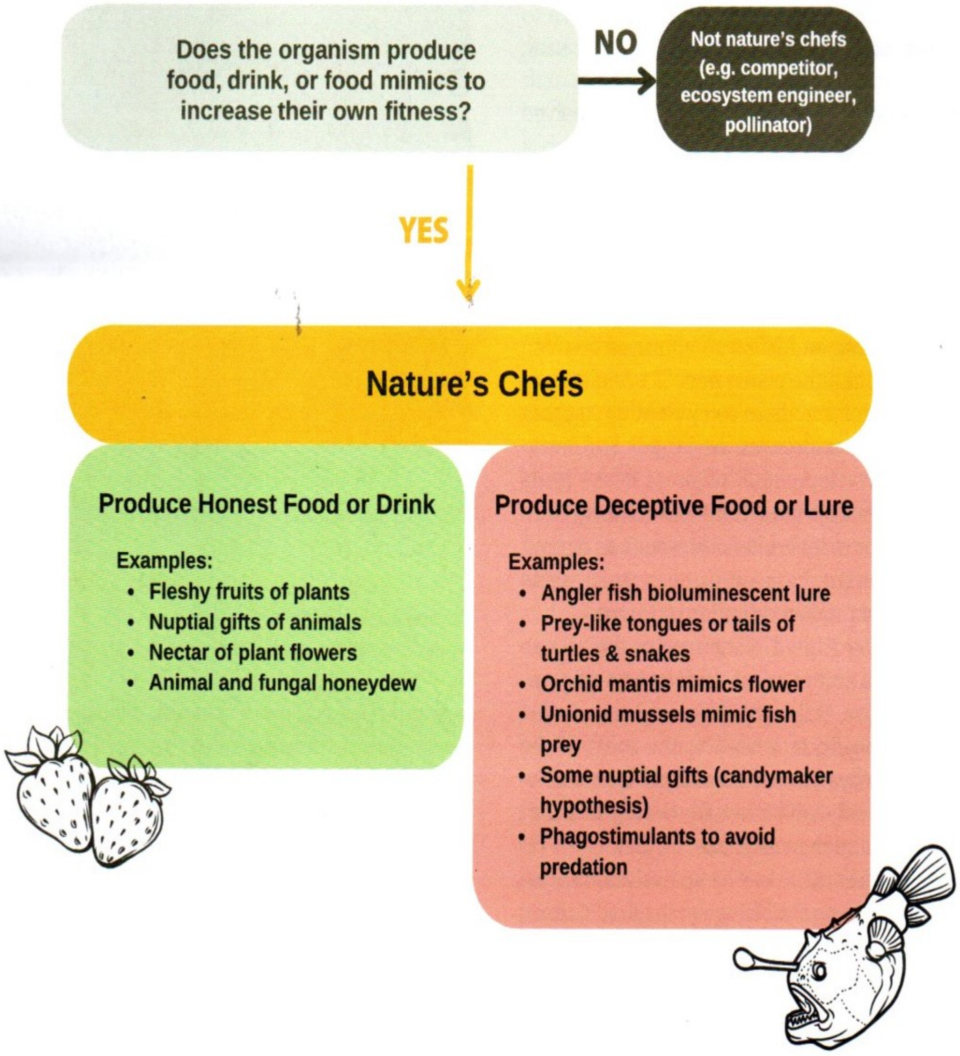

Figure 1. A simple decision tree for determining whether a particular case or species interaction might be considered under the Nature's Chef framework. That is, species that have evolved ways to produce or prepare food or drink items for consumers or diners or deceive other consumers that they are providing food or drink, so as to improve the success of their offspring and genes.

preparation is thought to have begun with modest food processing and sharing by our common ancestors with chimpanzees (e.g., specific plant or animal parts or products; Mcgrew 1975, Nishida et al. 1992, Wittig et al. 2014), followed by the early use of fermentation (Amato et al. 2021), fire (Wrangham 2009), and, much later, agriculture to alter the foods available to human consumers. These ancient human food preparers and sharers were not only shaped by the same ecological dynamics and evolutionary selective pressure that shape nonhuman food producers, but they also interfaced with food producers by consuming them. Therefore, the human story is not apart from the broader ecological and evolutionary story of food producers and consumers but, instead, is deeply intertwined with this story from its very origin.

As we consider food-producing organisms, we distinguish between species that attract animal consumers with honesty or deception and between what they offer: foods (e.g., fleshy fruits, nuptial gifts), drinks (e.g., nectar), and lures (e.g., angler fish bioluminescence; figure 1). These cases, or species interactions, do not previously appear to have been considered together. After describing the three ways organisms make and prepare food, we propose several future directions that deserve further study to evaluate how nature's chefs can serve as a concept to synthesize a subset of species interactions ranging from mutualism to predation. Throughout our work, we note the ways in which species that make, prepare, and share food are influenced by the sensory systems of their consumers and, vice versa, the ways in which the sensory systems of consumers have been shaped by those foods. We note that the evolution of traits associated with food or that mimic food to attract consumer species may have evolved because of phyletic or developmental constraints or, in some cases, for some other function; nonetheless, these traits may currently be under selection via the consumers they attract, which is the focus in the present article.

Plants with fleshy fruits

Plant species with fleshy fruits have been relatively well studied with regard to how they attract and satisfy (and sometimes deceive) consumers. Fleshy fruits and their functional equivalents (e.g., strawberries or figs, which we call *fruits*) are produced by many plant species. They have evolved many times independently with the radiation of angiosperm plants (Eriksson 2016). Their unique feature, as opposed to dry fruits (e.g., most grains, dandelions), is that the seeds are wrapped in a nutritious tissue whose primary function is to attract frugivores (fruit-eating animals) to consume them. Plants create their fleshy fruit during the process of development, in which unpalatable unripe fruits become attractive ripe fruits: The ingredients are transformed into a final product as chemical processes break starch into sugar (Giovannoni 2001), amplify attractive aromas (Nevo et al. 2018), and remove toxins, tannins, and other compounds that serve to make the immature fruit and seeds unattractive (Crozier et al. 2006).

The switch to biotic dispersal of seeds via fleshy fruits evolved convergently in many independent plant lineages along with a shift to shaded habitat, where competition for light favored larger, energy-rich seeds (Bolmgren and Eriksson 2010). This shift to energy-rich seeds created a paradox: Heavier seeds tend to land closer to the parent tree and suffer from increased mortality (Harms et al. 2000). Fleshy fruits are an evolutionary solution to this paradox: Animal patrons are lured to consume a nutritious and attractive resource, and the plants benefit when the animals swallow the seeds and release them away from the mother tree, providing the transport cost of even the largest and heaviest energy-rich seeds. The developmental origin of fleshy fruits differs widely among plant lineages (and even within them), from botanical fruits such as berries to inverted flowers such as figures, demonstrating a wide range of mechanisms through which natural selection has convergently produced similar solutions.

The diversification of fleshy fruited plant species appears to have triggered the diversification of some fruit-consuming animal species (Rojas et al. 2012, Eriksson 2016), which, in some cases, show evidence of coevolution related to the traits of the fruit species and the sensory systems of the animal species. Coevolution occurs when there is "an evolutionary change in a trait of the individuals in one population in response to a trait of the individuals of a second population, followed by an evolutionary response by the second population to the change in the first" (Janzen 1980). Diffuse coevolution occurs when these changes are among groups of species rather than just individual species (Janzen 1980). In most cases, the evolutionary relationship between fruits and consumers is diffuse. For example, the diversification of fruits appears to have led to the evolution of more complex color vision in some primates (including the ancestors of humans) which, in turn, shaped the ongoing evolution of fruit color (Onstein et al. 2020). The response of human diners to color appears to be a direct result of this coevolutionary dynamic.

Most fleshy fruits and other fruit-like bodies have not evolved to attract any particular species of consumer but, instead, to attract groups of disperser consumers. In other words, fleshy fruits have dispersal *syndromes*, where similar features attract similar dispersers that are united by their shared sensory systems (Valenta and Nevo 2020). For example, large fruits such as avocados, papayas, apples, and durians have repeatedly evolved traits that attract and please large mammals as their dispersal agents (Guimarães et al. 2008); their attributes, as a result, typically appeal to the visual, olfactory, and taste preferences of mammals. Conversely, conspicuous colorful displays are common in fruits such as raspberries, blueberries, cherries, or chili peppers, whose main seed dispersers tend to be day active and possess an elaborate color vision system. These include birds but also a subset of primate species (Onstein et al. 2020). Particularly aromatic fruits tend to cater to animals that rely on their sense of smell (Valenta and Nevo 2020). Plants dispersed by ants (of which there are tens of thousands of species; Lengyel et al. 2010) tend to have seeds with tiny fruit-like appendages called *elaiosomes* that often smell like prey items or cadavers (Borges 2015). The degree of specialization of specific guilds of frugivores stems from the reality that consumers differ in their learned and innate sensory systems and preferences. Compared with the diversity of fruits, human chefs cater to a narrow range of consumers, with sensory systems that differ but typically in comparatively modest ways as a function of genetic differences in taste receptors (e.g., Soranzo et al. 2005, Shepherd 2011) or experiential differences associated with olfactory learning, for example.

Fruit and behavior

Fruits benefit when certain consumers ingest them and deposit them in favorable settings that are more favorable than the sites beneath their maternal plant. They also sometimes benefit when those consumers carry out specific behaviors. As a result, natural selection has, in some cases, favored the evolution of fruits that alter consumer behavior after consumption. For example, some epiphytic mistletoe fruits are sticky, even after being voided in the feces of a consumer. This causes the consumer—often a bird—to have to wipe its feet on a branch to detach the seed from itself. This causes the seed to be more likely to be deposited on a branch, where it can grow into its host tree, rather than on the ground, where it will die (Reid 1991). Other fruits produce laxatives so that their seeds are quickly voided by consumers before they are partially digested (Murray et al. 1994). We know of no examples when it is beneficial for primates, including humans, that offer food to do so in such a way as to result in sticky feces or laxative-like effects. However, some plants that have been domesticated by humans could be argued to have favored—through their sweet rewards—human behaviors that led to their domestication. It has been argued, for example, that corn was first domesticated for their sweet stalks; plants that produced sweeter stalks were more likely to be consumed and planted and, therefore, were more fit (Smalley and Blake 2003).

In addition to fleshy fruits, some plants, animals, and fungi produce other fruit-like bodies in exchange for services provided by animals. The best studied examples may be the fat bodies that plants produce to attract ants that can defend the host plants from herbivores (Davidson and McKey 1993). Similarly, multiple lineages of stick insects have evolved egg cases with an appendage that attracts ants: The ants consume the appendage and then transport and deposit the egg case in their rubbish pile, where it is typically protected from harsh environmental conditions and predation (Hughes and Westoby 1992). There is also the incredible diversity of fungal fruiting bodies (aka mushrooms), with spores that can survive the digestive process when consumed by animals (Stephens and Rowe 2020). So far, as is currently understood, the general features of the evolution of fruits discussed above also apply to these fruit-like bodies.

Nuptial foods

Our interdisciplinary approach allows us to unite methods by which plants woo consumers and those by which animals do the same—concepts that have been almost exclusively studied by different scholars using separate bodies of theory. Consider nuptial gifts. Oral nuptial gifts are resources that (in addition to gametes) are prepared and offered by one organism, usually the male, to another for consumption during courtship and mating (Boggs 1995). Just as with fruits, the visual presentation, aromas, tastes, and quality of oral nuptial gifts are important. As such, within species, the coevolution between nuptial food gift producers and postcopulatory preferences by gift receivers has been shaped through sensory exploitation of the normal gustatory and other sensory systems (Sakaluk 2000). In contrast to fruits, nuptial gifts are a food item that serves as a measure of a potential mate and are therefore shaped both by natural selection and sexual selection, with targets of selection including both foraging and reproduction. Furthermore, nuptial gifts are food provided to

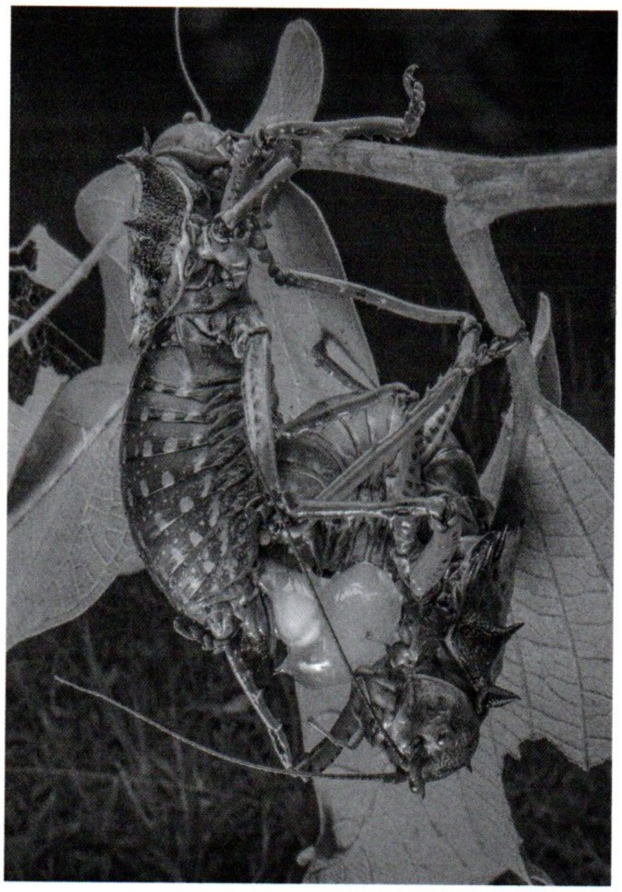

Figure 2. A male of the katydid *Enyaliopsis iaculator*, on the bottom right, produces a nuptial gift—termed a spermatophylax—the female, top left, hangs on to the branch. The female will reposition to taste and consume the gift. Photograph: Piotr Naskrecki, taken in Gorongosa National Park.

intraspecific organisms, whereas fruits are provided in interspecific interactions.

Oral nuptial gifts differ, one from another, in their method of preparation. Some nuptial gifts are made by males using their bodily resources (e.g., salivary and anal secretions, seminal fluid proteins, amino acids, body parts) and offered to females before or during copulation (Lewis and South 2012). For example, male cockroaches prepare a nuptial food gift for females that constitutes an important nitrogen source for the female and her eggs (Schal and Bell 1982). In other species, males create nuptial gifts by procuring resources from the environment, such as seeds or prey; these food items are then offered to the female to attract, initiate, or prolong copulation (Lewis and South 2012). Some male spiders present potential mates with prey items wrapped in silk (Brum et al. 2012). Gulls, terns, and skuas participate in courtship feeding, where males bring fish to potential mates, demonstrating not only their own fitness but also their ability to feed chicks (Wiggins and Morris 1986). The ultimate benefit females derive from the nuptial gifts may often be nutritional. However, as with fruits or nectar, the proximate choices consumers make are typically (perhaps invariably) guided by sensory preferences. As an example, female spiders of the species *Paratrechalea ornata* have been shown to prefer gifts that possess specific tastants (Brum et al. 2012). Animals that produce nuptial gifts sometimes even tailor them so as to increase their chance of being consumed. Evidence from orthopterans (grasshoppers, crickets, and katydids) shows that female consumers choose males who incorporate phagostimulants into their spermatophylax that attracts, enhances taste, and sustains feeding (figure 2).

In primates, gifts of food are often also given, although among primatologists, this act is typically described as *food sharing* rather than *gifting*. Contrary to earlier hypotheses, foods that are prized by chimpanzees because of their tastes (Dunn and Sanchez 2021), including monkey meat and honey, do not appear to be traded for sex as nuptial gifts (Gilby et al. 2010). However, they are often shared in ways that structure and are structured by social interactions. For example, food sharing has been shown to be associated with the release of oxytocin and is thought to reinforce social bonds (Crockford et al. 2013). As a result, food sharing in chimpanzees might be described as *prosocial gifting*. Similar prosocial gifting in the common ancestors of humans and chimpanzees is thought to be the root of the origin of more complex food preparation and sharing behaviors in modern humans (for a review, see Jaeggi and Gurven 2013).

In general, selection favors species that make, prepare, or share food so as to maximize their fitness benefit while minimizing the energy costs of food preparation (Lewis and South 2012). As a result, like plants, animals that produce nuptial gifts can and do cheat their consumers: The gift producer can increase its own reproductive success by providing a cheap snack disguised as a higher-quality nuptial gift. Some nuptial gifts deceive consumers by providing compounds that trigger taste receptors or other biases or preferences of the sensory system, without providing comparable nutrition (figure 1). This phenomenon is referred to as the *candymaker hypothesis* (Warwick et al. 2009). The nuptial gifts of dance flies are highly visible but empty silk balloons, which appear to be visually stimulating even though they provide no reward (Sadowski et al. 1999). Cheating is presumably used more frequently by nuptial gift givers than fruits or nectar (below) because of the low probability of repeated interactions and, therefore, punishment of cheaters. Indeed, sexual conflict theory predicts that natural selection should favor the evolution of males that reduce their investment from costly nuptial gifts (e.g., edible items) to less valuable items (i.e., inedible items; Sakaluk 2000). The observed evolutionary progression of the nuptial gifts of empidid flies, for example, shows decreasing investment from insect prey items to silk-wrapped insect pieces to an empty silk balloon that may even be reused. Therefore, cheating can be a successful strategy as long as the gifts (edible or inedible) are accepted by females and stimulate copulation long enough for sperm transfer (Lebas and Hockham 2005). In this context, the females are expected to be under strong selection to evolve the ability to distinguish between rewarding and unrewarding gifts, with the potential for male cheating to drive female sensory evolution (Albo et al. 2011).

Flower nectar mixology

Mixology is the study of how best to mix drinks so as to suit consumer preferences. A key dimension of the response of flowers to consumers relates to the evolutionary response of the composition of nectar to the sensory systems of the consumers that drink nectar. Pollinators are attracted to many plants by various mechanisms, including sugar-rich nectar. While drinking nectar, pollinators are coated in pollen that they then carry to subsequent flowers when seeking more nectar. Importantly, nectar in one flower is, like human drinks, typically not enough to fully satisfy the consumer. Nectar rewards are typically quite simple and standard, with variation in sugar and amino acid composition and concentration. However, even simple variation in nectar sugar composition does associate with visitation by particular taxa of pollinators. For example, primarily hummingbird- and moth-pollinated flowers have a lower proportion of hexose in their nectar compared with bee-, bat-, and fly-pollinated flowers (Wolff 2006). Moreover, variation in nectar sugar concentration influences viscosity enough to be differentially selected by bird versus insect pollinators (Kim et al. 2011, Rico-Guevara et al. 2015). For example, insects that feed by dipping their tongue in nectar typically visit flowers with higher nectar sugar concentrations (35%) that are more viscous compared with the nectar sugar concentrations (20%–25%) of flowers visited by birds and butterflies that use suction feeding (Heyneman 1983). Moreover, recent work suggests that concentrations of nectar amino acids below detection thresholds may still enhance a hummingbird's response to nectar sugars, a subtle synergistic effect representing a novel way plant nectar composition can select specific pollinators (Cockburn et al. 2022). Furthermore, divergence is evident among flowers themselves, which serve as an advertisement for the drink (Raguso 2004). Floral displays also have commonalities with food plating, which is to say the physical arrangement and presentation of food on a plate, because they are part of the sensory experience directly associated with the consumption of the drink. In the present article, we focus on flowers as plating but note that it is also interesting to think about and compare them with other forms of food advertising.

Plating of food and drink

Studies of human chefs have shown that the arrangement, color, and, more generally, presentation of food on a plate—termed *plating*—has a strong influence on consumer satisfaction (Gabrielsen et al. 2009). Similarly, visitation to nectar sources is strongly influenced by the scent, shape, and colors of flowers. For example, augmentation of floral scent in dame's rocket flowers increases pollinator visitation in general, and plants that naturally emit more scent have higher fitness (Majetic et al. 2009). In mustard, the differing sensory systems—and, therefore, the preferences—of bumble bee and hoverfly pollinators drive divergent evolution among mustard lineages for flower visual appeal and particular floral scents (Gervasi and Schiestl 2017).

The degree of specialization of specific pollinators seeking nectar varies much more than that of fruits seeking dispersers. Some flowers are generalists, catering to pollinators with diverse sensory systems and preferences and, therefore, part of diffuse evolutionary and sometimes coevolutionary dynamics. We predict that generalist flowers must provide cues that respond to relatively conserved aspects of sensory systems; this is likely to especially be the case for flowers that appeal to both vertebrates and invertebrates. Other flowers attract specific pollinator guilds, on the basis of a combination of traits that scientists have described as floral syndromes, akin to dispersal syndromes. For example, tube-shaped flowers that are open during the day are likely to be pollinated by birds and are thought to have evolved these traits in response to bird morphology and activity patterns (Fenster et al. 2004). Similarly, flowers that are pollinated by phyllostomid bats typically produce sulfuric compounds, which are thought to be effective long-distance cues at night for pollinators that depend less on vision (at a time of day when visual cues are less apparent; Raguso 2004). More rarely, flowers specialize on particular bee species that have narrow preferences with regard to pollen chemistry (oligolectic species); these flowers can be predicted to have morphologies, aromas and other characteristics that have evolved in response to the sensory systems of those bees (e.g., Shimizu et al. 2014).

Figure 3. A dish from El Celler de Can Roca, called "Macadamia rose, grapefruit, lychee, and Jordi Roca's nose" illustrates similarities between plated food and flowers. In this case, the flower petals are made of macadamia nuts. Photograph: El Celler de Can Roca, Joan Pujol-Creus.

Flower presentation is a case in which there is the potential for human chefs to learn directly from ecologists—in this case, from the methods of ecologists. Studies of human food plating have shown that consumers intuitively prefer complexity (figure 3). For example, student subjects in a lab setting prefer when the culinary elements of a dish look like an abstract-art painting on the plate (Michel et al. 2014). In other cases, consumers have been shown to have preferences for an aesthetic plating such as one that features oblique lines ascending to the right on the plate (Youssef et al. 2015). Another study showed that the intensity of the color in the presentation of a dish affected diners' perception (liking; Piqueras-Fiszman et al. 2013). To date, these studies have been relatively coarse with regard to the effects they could discern. Studies of flower preferences have been able to consider more nuances. For example, a recent study of *Dracula* orchids, which mimic mushrooms and, as a consequence, attract mushroom-feeding flies that then pollinate the orchids, used a combination of real flowers and three-dimensional realistic artificial flower components printed using scent-free surgical silicone. Scents could be added to the silicone. Using this design, scientists were able to add and subtract individual elements of the *Dracula* flower's visual presentation and its aroma. In doing so, they identified that the aromatic components largely served as long-range advertising signals (perhaps akin to a billboard), whereas certain visual components contributed to the flies' attraction at close range (Policha et al. 2016).

Drinks are common in the plant kingdom; they are rarer but nonetheless exist among animals and fungi. Honeydew is produced by many Hemiptera (true bugs) and Lepidoptera (butterfly and moth) species (Way 2003) and even some fungi (Beerwinkle et al. 1993). For example, aphids consume plant phloem with a physiologically high sugar content and osmotic pressure, then transform the excess sugar into a physiologically less extreme substance containing long-chain oligosaccharides and essential amino acids, called *honeydew*, which is offered and consumed by other animals. Many ants cultivate mutualistic relationships with honeydew producers, collecting excreted honeydew or behaviorally inducing producers to excrete honeydew in their presence (e.g., ants will stroke aphids with their antennae to induce them to release honeydew; Andrews 1930). In exchange for the drink, most consumers of honeydew provide indirect defense against predators and parasites of the honeydew producers. Although ants are perhaps the best known honeydew consumers, some other insects (e.g., native bees when flowers are scarce; Koch et al. 2011), vertebrates (e.g., Madagascar geckos; Fölling et al. 2010), and even fungi also take up honeydew (Dhami et al. 2013)

Lures

Some species lure consumers with apparent food rewards and then do not provide the consumer with any benefits. Sometimes, these lure-producing species trick their consumers into providing a service. More often, they consume them. These deceptive food producers can be found among animals, plants, and other taxa but appear to have never been considered synthetically (figure 1). Deceptive food producers often use olfactory cues, visual cues, or both to lure would-be consumers. In rarer cases, they use tactile cues (e.g., some spiders manipulate the webs of other spider species to mimic prey, then eat the web-creating spiders). These deceptive food producers are the opposite of Batesian mimics; instead of resembling an unpalatable species, they resemble other nutritional or tasty species and thereby mimic deliciousness. Deceptive food producers also differ from species that provide an honest meal, because, in addition to preparing a presumptive food, the deceptive food producers are usually the consumers.

In animals, there exists a bestiary of species and, indeed, lineages that are entirely deceptive with their food-like lures. For example, lures exist in anglerfish (which lure prey using a bait-like structure hanging in front of its eyes and mouth; Gudger 1945, Pietsch and Grobecker 1978), water snakes and alligator snapping turtles (which lure their prey with their worm-like tongues; Welsh and Lind 2000, Hansknecht 2008, Drummond and Gordon 2010), copperheads and other vipers (that lure their prey with their tails when young, tails that even sometimes fluoresce; Paul and Mendyk 2021), Jackson's chameleons (which lure insect prey by applying a sticky substance located in their jaw pouch onto branches, then capturing flies landing on or near the substance, which has volatile odors similar to insect pheromones; Preest et al. 2016), and orchid mantises (which mimic a generalized flower-like stimulus and lure in pollinating insects; O'Hanlon et al. 2014). Deceptive food producers can also use false food cues, or *phagostimulants*, as lures to escape predators (*phagomimicry*), such as the chemical compounds (e.g., taurine) emitted when a sea slug inks and spiny lobsters react with both appetitive and ingestive behaviors by digging into ink-covered sediments or moving appendages toward their mouth (Derby 2007). One might predict that deceptive food producers would trigger the evolution of their prey to detect their subterfuge. However, we predict this is only likely where the deceptive food producers are a common predator of the particular prey species and, therefore, a strong selective pressure, but prey could also become less discriminatory of lures if other types of legitimate food are abundant (Kloock and Getty 2019).

Some of nature's most extraordinary deceptive food producers can be found among freshwater mollusks in the family Unionidae (aka the pearly mussels; Haag and Warren 1999. Freshwater mussel larvae are obligate external parasites of freshwater fish, with a mussel species relying on single or several fish species for a portion of their life cycle (Barnhart et al. 2008). The larval stage must attach to the gills or fins of specific host fish species where they remain for days or weeks until metamorphosis into juvenile mussels and then release from the fish. Adult mussels are not highly mobile relative to a fish, so freshwater mussels have evolved a way to bring fish closer: They make lures that look like the host fishes' prey (figure 4; Haag and Warren 1999, Barnhart et al. 2008). Natural selection has produced mussel lures that aggressively mimic the prey of hosts and, in doing so, attract fish close enough so that offspring released by the adult mussel can attach to the fish rather than float away. To be maintained, the frequency of legitimate meals from real prey (i.e., model) must be high enough to allow deceptive food producers (i.e., mimic) to persist. It is likely that interesting evolutionary dynamics exist as a function of the relative frequency of deceptive food producers and the species they mimic. These dynamics don't appear to have been studied.

Examining luring strategies of mussels in a phylogenetic context provides several hypotheses for how lure strategies have evolved in response to both host fish foraging preferences and the energetics of lure production as selective agents (Zanata and Murphy 2006). In the lampsiline mussels, the active mantle flap lures (e.g., elaborate and moveable mantle lure tissue) evolved early, suggesting strong selection on the host-attraction stage in the life cycle of freshwater mussels. Mantle flap lures have been independently lost in several clades, as might be expected if the lures are energetically expensive and only beneficial in the presence of particular hosts (Zanata and Murphy 2006). In other mussel species, selection pressures to reduce the energy invested in lures has led to lures that are mucus packets of offspring, some composed of meter-long mucus strands with offspring tethered in a packet on the end that is dangled in flowing water and mimics swimming prey (Barnhart et al. 2008). In the most recently evolved *Epioblasma* species, there is minimal or no investment in the lure (Zanata and Murphy 2006). Mussels force "feed" larvae to their host fish by opening their shell and closing it on the host fish's head when it comes near, releasing larvae into the fish's mouth to ensure their offspring attach to the host's gills.

It is, as of yet, unclear whether freshwater mussels produce tastes or odors that mimic their host's prey. But quadruline mussels have uncharismatic, white-colored, motionless lures displayed only at night (Sietman et al. 2012) when their host catfish commonly feed using tactile and olfactory cues. Future research is needed to explore whether freshwater mussels have evolved water-borne odors that attract host fish and, if so, whether the odors are attractive to fish in general, are host species specific, or host prey species-specific odors.

Parasitic mussels are not the only animals that create lures that trick host species into becoming infected (i.e., foraging selection). Many helminth parasites transform their intermediate hosts in ways that increase susceptibility to being eaten by their final hosts. For example, a nematode that parasitizes ants causes ant gasters to redden and appear berry-like, potentially increasing the likelihood that the ants (and the nematodes in them) might be consumed by birds (Yanoviak et al. 2008). Similarly, the green-banded broodsac trematode causes snail antennae to change colors, swell, and pulse, appearing caterpillar-like to definitive bird

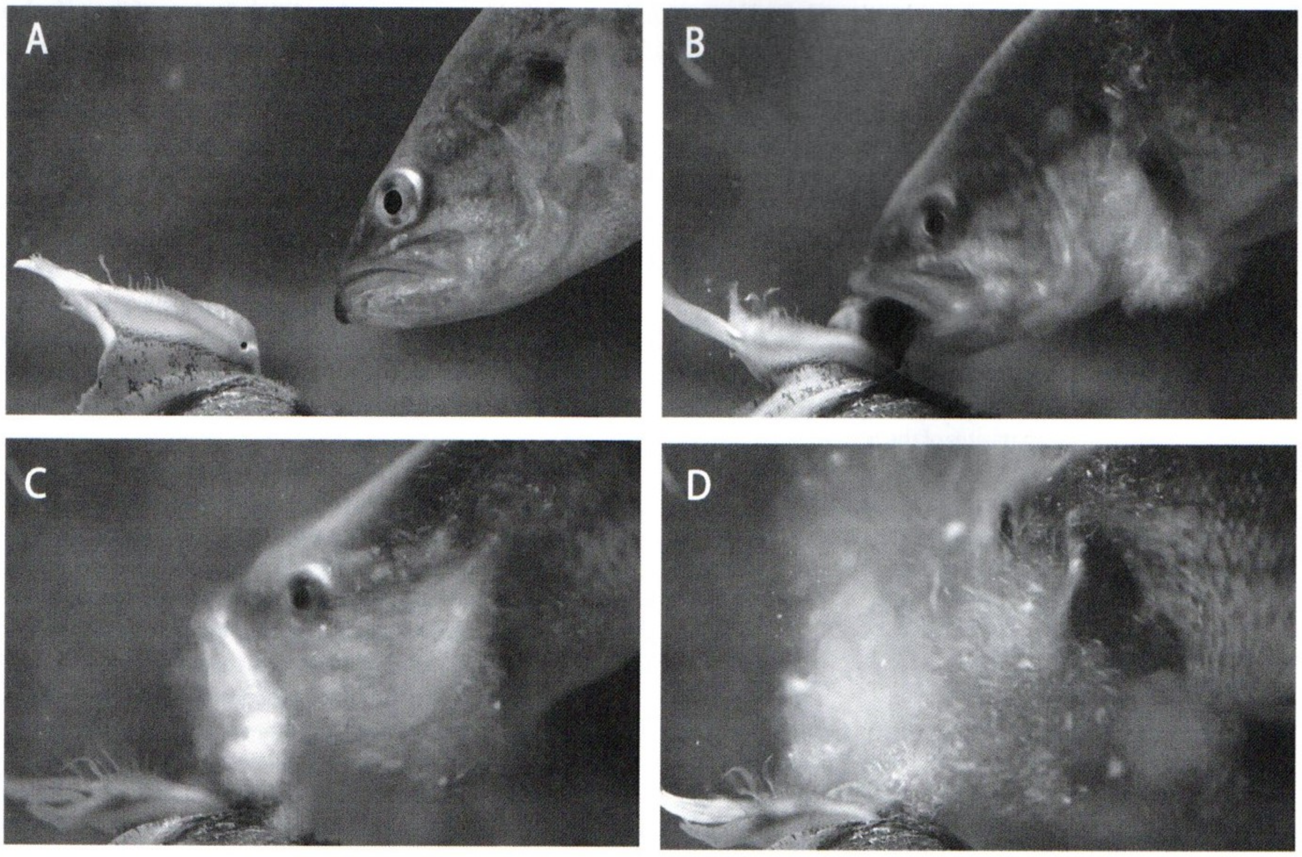

Figure 4. Freshwater mussels produce a visually appealing but false meal for their specific host fish, which has resulted in elaborate selection on female mussel's mantle flaps and marsupium to lure fish nearer as well as an array of mechanisms by which larvae are released to effectively attach to host fish gills. (A) Lampsilis mussels produce a fleshy structure that when displayed looks and moves like a small fish, which attracts specific host fish species near and females release a plume of thousands of larval offspring, coating fish in a faceful of the parasitic larvae. (B) In some cases, the lure elicits a direct physical attack by a host fish, and (C & D) the mussel, attack, or both result in effective transfer of the obligate larval parasitic stage (white cloud) to the host fish gills, but without the pleasures of ingestion. Photographs: Still images from a video by Brett Billings and Ryan Hagerty/USFWS.

hosts (Lewis 1977). Such cases are referred to as *parasite enhanced trophic transmission* (Lafferty 1999) and are actually intermediate between lures and fruits.

Meanwhile, some plants, such as carnivorous plants, produce lures, presumably to attract their putative prey. Carnivorous plants typically live in nutrient-poor soils and compensate for low soil-nutrient access by consuming insects. But how do they lure those insects to their traps? In the case of pitcher plants, *Sarracenia purpurea*, researchers used artificial pitchers to separate out the luring effect of pitcher color from that of sugars. Pitchers produce sugars on the rim of the pitcher's lip. Bennett and Ellison (2009) found that artificial pitchers without sugars on their outer lip collected few insects, whereas artificial pitchers with sugars painted on their outer lips collected similar numbers of prey as natural pitcher plants. Their study suggests that these plants lure unsuspecting prey via this sugar source. Other carnivorous plants may use scent or scent mimics (i.e., trap scent that mimics flowers) to lure prey (Di Giusto et al. 2010, Kreuzwieser et al. 2014). For example, fungal odor mimicry by Jack-in-the-pulpit plants attracts obligate fungus-eating insects, which are tricked into visiting male flowers where they are covered in pollen, then pollinate female flowers where they are trapped in the pulpit and consumed (Ellison and Gotelli 2009, Kakishima et al. 2019). Indeed, the striking diversification and evolution of botanical carnivory can be explained by rapid morphological evolution in genes responsible for the high energetic demands of insect traps (Ellison and Gotelli 2009).

Lures aren't limited to baits that are wiggled enticingly to animal consumers. In plants, lures can be found among deceptive fruits and flowers. For example, a relatively common African tropical plant, *Pentadiplandra brazzeana*, produces berries that contain virtually no sugar but, instead, tiny amounts of a protein, brazzein, that tricks the sweet taste receptors of most primates, including humans, by interfering with the mechanism of the receptor (Guevara et al. 2016). Brazzein is almost 2000 times sweeter than sucrose (when compared by weight), requiring only a small production of the protein to elicit feeding and dispersal by most primates. At least five sweet-tasting proteins similar to brazzein have been discovered, each evolving independently in places where there is hypothesized to be a selective advantage for the plants in using primates as seed dispersers (Guevara et al. 2016, Neiers et al. 2018). In gorillas, the negative effects of consuming these fruits (via time lost feeding on more nutritional food items) appears to have been sufficient so as to trigger evolution in gorilla sweet taste receptors. Gorillas no longer perceive *Pentadiplandra brazzeana* fruits to be sweet. A similar case has been documented in the plant, *Ceratocaryum argenteum* (Restionaceae). Seeds of this plant species are visual and chemical mimics of herbivore scat; they lure dung beetles to disperse and bury them, enhancing their own fitness but leaving the beetles hungry and frustrated (Midgley et al. 2015). Similarly, orchids, particularly the slipper orchids (Cypripedioideae), produce a variety of odors and structures that mimic diverse foods (e.g., fungi, carrion, dung), which lure specific insect pollinators, including fruit flies, dung flies, and a fungal spore-eating hoverfly, often without providing a reward (Pemberton 2013). Indeed, *Cypripedium fargesii* orchids fool hoverflies (Syrphidae) into pollinating their flowers by producing both odors that smell like *Cladosporium* fungi, as well as foliage structures that mimic the fungi's spores that are eaten and dispersed by the fly (Pemberton 2013). In each of these cases, the production of false foods is predicated on the reduced cost, whether in carbon or particular elements, of producing features that stimulate consumer senses compared with the cost of producing whole food items.

To our knowledge, there exists no comprehensive review of luring behavior in nature (e.g., deceptive fruit, flowers, animal lures). However, the examples we have noted raise several questions. First, what do animal and plant lures have in common with the presentation of foods by human chefs? As such, is the taste or odor of lures important to potential consumers or is it mostly visual presentation?

Future directions

Having provided some examples of the ways in which organisms make, prepare, and offer food, we now identify several phenomena that deserve further holistic attention with regard to these species. These are phenomena that we think have been understudied because the instances in which organisms make, prepare, and share food have been studied in isolated disciplines.

Taste and ecological stoichiometry.

Generally speaking, we hypothesize that one dominant framework for understanding food-producing species is ecological stoichiometry. Animal sensory systems (and especially taste) evolve to reward animals for finding what, on average, is needed to balance their ecological stoichiometry (e.g., to obtain enough key elements to make more of their cells and fuel their cells; Demi et al. 2021). Animal taxa and trophic levels differ predictably in their needs and, therefore, the details of their taste receptors (e.g., carnivores often lack sweet taste receptors; Jiang et al. 2012). Food-producing species must account for the receptors of their preferred consumers during evolution. Such accounting is likely to respond to coevolutionary dynamics over time. For example, fruits that attracted the ancestors of felids would likely have benefited from being sweet. However, once that ancestral felid lost its sweet taste receptor, the benefits to the fruit of continuing to be sweet would be greatly reduced (Li et al. 2005).

Over evolutionary timescales, we predict that ecological stoichiometry is key to understanding the evolutionary dynamics in general, and coevolutionary dynamics in particular, of the food produced by organisms and the sensory systems of their consumers. The elements in the foods that organisms produce can be assembled, via natural selection, to yield different tastes, odors, shapes, textures, etc., to attract and elicit the consumer to return. Which types of foods are produced, however, will ultimately be determined by the sensory preferences of consumers (e.g., Albrecht et al. 2018), which are, in turn, influenced by the stoichiometric needs of those consumers. In this light, the study of consumers with unusual stoichiometric needs or sensory systems might be particularly illuminating. For example, how do food-producing species respond to consumers that don't have taste receptors at all (Jiang et al. 2012)?

A second level of ecological stoichiometry is that food-producing species must balance what they produce with what they have. Where nitrogen is rare, plants are limited to making food for animals rich in nitrogen while still making more of their own cells, for example. We hypothesize that this partially explains why fruits that mimic animals are rare (though imagine a tree covered in fruits that look and smell like mice). Likewise, animals crave salt and need it to maintain electrolyte balance, but plants do not, so it is in low concentration in most fruits and, therefore, an ecological stoichiometric constraint of plants that produce food. Similarly, human chefs are limited by available local and seasonal ingredients, which form the basis of cuisines around the world. The traditional cooking of Sri Lanka and Scotland vary widely on the basis of regionally available ingredients, but both produce food that is nutritional and flavorful to the human palate. A recent trend among contemporary chefs makes a point of using local limitations to push the limits of culinary creativity. A chef in the Nordic cuisine movement, spearheaded by the restaurant Noma, in Copenhagen, may forgo using imported lemon and, instead, add acidity to a dish with sour-tasting wood sorrel or gooseberries, both locally common (Redzepi 2010). Other chefs, such as Virgilio Martinez in Peru and Selassie Atadika in Ghana, similarly focus on creating novel dishes with local ingredients; examples include edible cyanobacteria (kushuro) from Peru's high-altitude wetlands and Ghanaian okra as a thickener in soups and stews (Martinez and Gill 2016).

Meaty fruits

In the long run, we hope that the interdisciplinary consideration of food-making, -preparing, and -sharing organisms facilitates conversations across disciplines with regard to food and eating, consumers and producers or chefs, and about species interactions. One such conversation occurred at the aforementioned Talking Sense meeting. A key theme was how one might learn from nature to produce plant-based foods that have meaty flavors. This led one of us (RRD) to wonder whether there are plants in nature that mimic meat to attract carnivores. If so, it would be straightforward to study and learn from such plants to develop new culinary approaches. But we found few direct references to plants that have evolved to attract carnivores, which does not mean such fruits or their carnivores do not exist or did not exist at one time. The exceptions are interesting but tend to be poorly studied. Avocados have been noted to attract felids, particularly when planted as orchards, and even cats as big as jaguars have been seen consuming the fruits (Borchert et al. 2008). Durian fruits have been argued to be dispersed by tigers; could their aroma in part mimic that of putrefying meat? Such a possibility is suggested by the abundance of sulfur-containing compounds in durian that are also present in meat (Wong and Tie 1995). Ant-dispersed seeds, as we've already noted, often smell like dead insects. Ginkgo fruits (which smell a little like durians) have been argued to be dispersed primarily by carnivores (Zhao et al. 2010). So too are a number of lesser known tropical Asian fruits thought to be dispersed by civets (Nakashima et al. 2010). These cases deserve further study, but so too does the question of why carnivore dispersed fruits are not more common. It may be that carnivore fruits are more expensive to make, inasmuch as they are likely to require scarce nitrogen, phosphorus, and even sulfur to attract and sate carnivores (see the discussion of ecological stoichiometry above). Alternatively, the relatively acidic stomachs of carnivores (Beasley et al. 2015) might be more likely to kill seeds (although humans have extremely acidic stomachs and are effective dispersers of many seeds). A third possibility is that, because carnivores tend to be rarer than, for example, herbivores, they are relatively less reliable dispersers (if this were the case, one might expect carnivore-dispersed fruits to be stronger smelling to attract carnivores from farther away). Finally, some carnivores have lost most of their taste receptors (sweet, umami, bitter, and sour in cetaceans) and may simply rely on movement as a primary sensory cue for what to eat or, more precisely, what is meat.

Regarding plant-based foods that taste like meat, it is noteworthy that the food industry is investing in ways to transform and process plants (e.g., genetic modifying yeast to produce soy-based leghemoglobin) into something that looks like and tastes like meat (Goldstein et al. 2017). However, parallels with food-producing nonhuman species seem to be rare (e.g., symbiotic zooxanthellae provide amino acids to corals for protein synthesis). Why is this, and what are the consequences?

Sex and danger

A key general principle is that of exploitation of preexisting bias, wherein food-producing species cater to preexisting sensory biases of consumers (Zhao et al. 2010). Even relationships between food species and consumers that become coevolutionary may ultimately begin via exploitation of such biases. This is important because it suggests a general hypothesis—namely, that consumers with unique sensory abilities and biases might prompt evolutionarily unique responses by nature's chefs. For example, in addition to aroma per se (which is to say, aroma detected by olfactory receptors), many animals also have vomeronasal organs. Humans are currently thought to lack these organs (although there is debate; Stoyanov et al. 2018). These organs detect sex-associated pheromones. They also detect danger signals, whether they be the odor of a predator or the smell of death. The valence of chemicals that this organ intercepts appears hard wired; sex pheromones are liked. Danger cues (e.g., the smell of cat urine for mice) are disliked and avoided (Li and Liberles 2015). To what extent do food-producing species co-opt these innate sensory biases? European truffle species are often described as taking advantage of the sexual signaling (and, therefore, vomeronasal systems) of pigs and, indeed, do produce the key chemical in pig pheromones (Claus et al. 1981). However, the pig–truffle relationship remains poorly explored, and other studies suggest roles for other volatile compounds (Mustafa et al. 2020).

Movement and appearance

One feature of the appeal of food-producing species that has been little studied is the extent to which movement itself is appealing. Cats will kill prey even after they are full; presumably, doing so generates some pleasure (Biben 1979). Similarly, despite lacking taste receptors, dolphins are selective in what they eat, likely relying on visual or auditory cues (Spitz et al. 2010, Feng et al. 2014). As was noted, many fish seek out lures of various sorts (mimics of prey appearance, scent, or movement). In the present article, movement is interesting in that most lures in nature tend to move or to look very much like prey items (e.g., mussels and anglerfish). However, toads will strike repeatedly at a line drawn on a notecard if it is moved across their field of vision but will ignore the notecard if it is rotated 90 degrees so the line is vertical (Ewert 1987). For toads, apparently, a simple horizontal line is enough to stimulate the palate. Similarly, for humans, simply viewing food pictures induces satiation for similar foods sharing the taste or flavor aspects (e.g., salty) but not other foods (Larson et al. 2014). How might food-producing species use such sensory stimuli to induce satiation and minimize consumption? Or consider the many vipers that sport highlighter-yellow tails (some bioluminescent), which they flick rhythmically to entice frogs and lizards to draw nearer (Heatwole and Davison 1976). The evolution of both the bright color and the movement suggests that the prey of these snakes have innate preferences for food items that are both bright and wriggly. What can human chefs and agriculturalists learn from these examples to make new or more sustainable foods?

Mouthfeel

Human chefs often discuss mouthfeel (e.g., see the recent book on the topic; Mouritsen and Styrbæk 2017). Ecologists and evolutionary biologists also write about mouthfeel, but they tend to do so with regard to features of potential foods that lead them to have bad mouthfeels, such as prey defenses, spines, raphides in *Vanilla* fruits, or toxins and their relation to bitter taste receptors (Dodson 1974, Milewski et al. 1991, Eisner and Aneshansley 2000, Fürstenberg-Hägg et al. 2013, Gilbert, Pansarin 2018, 2021). However, nonhuman animals also have the ability to appreciate foods with pleasing mouthfeels. It seems possible that, for some foods, nature caters to the mouthfeel preferences of consumers. In the present article, two interesting examples stand out. First, avocados, although initially thought to have historically been dispersed by giant sloths (before the Clovis megafauna extinction; Janzen and Martin 1982, Barlow 2008) are now known to be quite attractive to wild cats (Borchert et al. 2008). Is it possible that the unique mouthfeel of avocados and relative lack of taste and aroma (humans often describe avocados as having a "green" flavor) evolved to attract predators. This hypothesis remains to be tested. A second case is that of jackfruit. Jackfruit are typically described in a modern context as being dispersed by large fruit-eating animals (and elephants do like them), but it is noteworthy that dining studies show that, when consumers are given jackfruit (without knowing what it is), they think, because of its mouthfeel, that it is meat (Uruakpa et al. 2021).

The external milieu

It appears that food-producing species differ depending on whether they are terrestrial or underwater; in general, food-producing species seem rare underwater. Although some animals produce lures that mimic foods, the equivalents of fruits and flowers seem to be rare, or at least rarer, underwater, as is animal-mediated pollination (Sculthorpe 1967, Lavaut et al. 2022). An exception is the seagrass, *Thalassia testudinumone* (turtlegrass), which produces flowers pollinated at night by invertebrates (van Tussenbroek et al. 2016) and fruits eaten by turtles (Falcón et al. 2019). Fruits and seeds of some other aquatic plants are consumed by migratory waterfowl and other birds (Sculthorpe 1967), as well as humans (e.g., the water chestnut, *Trapa natans* L.; Dénes et al. 2012), but compared with terrestrial fruits, we know less about these interactions.

More common are cases in which freshwater or marine animals eat terrestrial fruits, such as fruit-eating crocodiles (Platt et al. 2013) and fish (Goulding 1980, Correa et al. 2007). In the present article, we find that both water and fish select for fleshy fruits, the former for buoyancy and dispersal, or *hydrochory* (Correa et al. 2017), and the fish for taste and nutrition, as well as a preference by many fishes for neutrally buoyant foods. Notably, most seeds (78%) are viable after gut passage (Anderson et al. 2009), and, therefore, fruit-eating fish, like terrestrial frugivores, may influence seed dispersal (Anderson et al. 2011). However, beyond preferences for fleshy, floaty fruits (Correa et al. 2007, 2017) and fruit identity (in the broadest sense of the word) over availability (Araujo et al. 2020), what we know about selection with respect to fruits that fish or other consumers eat and their preparation for the aquatic realm by plants remains in untested hypotheses related to olfaction, vision, and the sound of fruits falling on the water. We find this surprising, because fish have taste receptors (even if cetaceans don't), and fish prefer some foods over others on the basis of taste (Kasumyan 2019).

However, despite these exceptional cases of marine fruits, aquatic pollinators and aquatic dispersal of terrestrial fruits, these cases are just that—exceptions. Comparatively fewer aquatic than terrestrial plants have evolved rewards or nutritious fruits. This absence is surprising—or maybe not, given that land plants evolved from aquatic ancestors. In addition, the mobility costs for an animal moving in water relative to air may exceed the nutritional benefits of fruit rewards from afar, especially given the abundance of suspended food in water relative to air (Vermeij and Grosberg 2010). Nevertheless, the contrast between the external milieu and especially the aquatic environment deserves further study, because food-producing species are common in water even though pollination and fruit dispersal seem to be rare.

Discouraging problem diners

Plants that produce sweet, fleshy, and brightly colored fruits whose seeds are dispersed by animals face a conundrum of attracting beneficial organisms while repelling harmful consumers. To this end, food-producing species may use directed deterrence, in which the production of plant secondary metabolites or other physical features are inhibitory toward organisms that destroy seeds but less so or not at all for seed dispersers (Cipollini and Levey 1997). Capsaicin and its subsequent hot, spicy flavor may have evolved to deter rodents and other vertebrates from eating chili peppers, but they do not deter birds that are not sensitive to capsaicin and are more effective seed dispersers (Tewksbury and Nabhan 2001). Furthermore, the desert plant *Ochradenus baccatus* (Resedaceae) has evolved directed deterrence that selects for rodents (typically, specialized granivores) to consume the fruit flesh and spit the seed, because chewing both combines chemicals of each, creating a toxic mustard oil bomb (Samuni-Blank et al. 2012). Eating the fleshy fruit and spitting the seed is done away from the plant, enhancing dispersal. Similarly, some flowers produce nectar that elicits a positive gustatory response by their preferred pollinators but that is distasteful to those with bill or body shapes ill suited to pollinate their flowers (Johnson et al. 2006). It is interesting to consider the extent to which catering to certain kinds of consumers and not others is present in both nonhuman and human food producers, as well as the general rules that govern when it is beneficial for a food producer to be more or less selective.

The behavioral food producers

In addition to cases in which food-producing species evolve so as to produce certain kinds of meals for consumers, a subset of these species actually behaviorally prepares food items. This includes some of the cases of nuptial foods already discussed (silk-wrapped prey items), but it also includes many other examples. Pikas (a small lagomorph) cache different but specific types of vegetation in hay piles for storage and consumption over the winter months. The vegetation types, including secondary compounds, often inhibit decomposition and spoilage of the hay (Dearing 1997a, 1997b). Hyenas, foxes, leopards, and other carnivores all store food, and the process of storage alters the microbial composition (Dunn et al. 2020). Some bees also store nectar and pollen, preferring the fermented stored food over freshly collected provisions (Vollet-Neto et al. 2017). Sapsuckers tap trees, like humans, and in the process, obtain calories from the sugars in the sap and protein from insects attracted by and trapped in the sap. Sapsuckers have even been observed dipping insects into sap before feeding them to their nestlings (Ehrlich 2023). Notably, this may be young sapsuckers' first exposure to sweets, which we now know they can taste (Cramer et al. 2022). In addition, some animals farm all of their food items, be it algae by damselfish (Lassuy 1980, Hixon and Brostoff 1983) or fungi by leafcutter ants and termites (Weber 1972, Mueller et al. 2005). Recent research has been focused on the nutritional exchanges between insects and their farmed species, particularly between ants and their fungi (Shik et al. 2021), whereas in damselfishes, there is a digestive basis for weeding and defense of monocultures of one particular algal species: They lack a gizzard and the digestive enzymes needed to digest most algae, except the edible species they farm and rarely found outside their gardens (Hata and Kato 2006). It is hard to imagine taste does not also play some role. However, less is known about the extent to which the choices these farmers make are mediated by the flavor experiences of their foods. Do ants and termites favor fungi, for example, that taste better than those that are available in the wild? We don't yet know.

Chefs might also attempt to manipulate the behavior of their customers. In nature, the consequences of consumer behavior after the meal can influence the food-producing species' reproductive success (i.e., the payment for the meal). In seed dispersal interactions, the seed is likely to suffer weaker density-dependent mortality if the consumer feels full (Janzen 1970) and satisfied and does not go on to ingest more and more seeds. It has been speculated that fruits may use various secondary compounds, which may also contribute to taste, to stimulate the consumer to end the meal (Cipollini and Levey 1997). This may parallel the strategy of many fast food restaurants, which provide a large and satisfying meal that is served and consumed fast to free up tables for the next customer. But other food-producing species have different fitness requirements and, therefore, different approaches: Successful pollination is achieved only if the pollinator stays long enough to passively collect sufficient amounts of pollen, which selects for many complex flower structures that prevent the consumer from acquiring the reward quickly. Even more critically, pollination is achieved only if the consumer goes on to visit another conspecific flower to deposit the pollen. This selects for flower-producing plant species that provide an attractive reward but one that does not fully satiate the pollinator, not unlike starters in a fancy multiple-course menu.

Warming food

Human chefs often employ heat not only to cook food but also to develop and feature the aromas associated with certain volatile compounds. For example, the aroma (and brown crust color) of grilled meat is caused by Maillard reactions that can only occur at temperatures well above boiling. A chef who cooks their meat sous vide (in a water bath at temperatures of approximately 45–70 degrees Celsius) in order to achieve a perfect texture throughout the meat will briefly sear it before serving to develop color and flavor (Roca and Brugués 2005). Similarly, the rich flavor of caramel is a result of sugar molecules breaking down into smaller volatile molecules at high heat. Similar phenomena exist in flowers, although they have not yet been terribly well studied. The dead horse arum, *Helicodiceros muscivorus*, lives on Mediterranean islands with seabird colonies. There, it relies on the blowflies that feed on dead seabirds as pollinators. The flowers look like dead animals and produce dimethyl sulfide, one of the aromas characteristic of dead animals (Raguso 2004), visual and olfactory cues to which blowflies respond. But these flowers also produce heat (as do the flowers of some other aroids). In the case of Helicodiceros, it has been hypothesized that the carbon dioxide produced (even if cetaceans don't), and fish prefer some foods over others on the basis of taste (Kasumyan 2019).

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Conclusions

The idea to consider food-producing species across taxa and circumstances stemmed from a statement that fruits evolved to attract seed-dispersing animals, which led to the realization that there has been no systematic and holistic study of organisms that produce food (or mimic food) for other organisms. In the present article, we offer a way to unite and classify a surprisingly common interaction in which selection has led to organisms that produce food or drink for other organisms or deceive other organisms by creating false food to ensure the success of their own offspring and genes. Such species are interesting to compare with humans but also include humans. The human ability to share and prepare food is a modern manifestation of an ancient evolutionary story. Food-producing species, including humans, can be viewed along a continuum from mutualism to parasitism or predation, whereby some provide food and drink in mutualistic or commensal relationships (e.g., fruits), some use lures as deceptive mimics of food in parasitic or predatory interactions (e.g., mussels and worm-like reptile tongues), some have formed symbiotic relationships, such as coral zooxanthellae, cellulose digesting gut bacteria, and endomycorrhizal fungi (all omitted for brevity in the present article). In the context of this diversity, we presented many new questions, hypotheses, and predictions surrounding the biology of food-producing species. Although we offer many future directions, we also wonder what new discoveries and mysteries we have not thought of in the present article that the study of food-producing species might generate within ecology and evolution, across disciplinary boundaries of food and culinary sciences, culinary arts and food industries, and for how we think about food.

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Disclosure statement

The authors declare no conflicts of interest.

References cited

Albo MJ, Winther G, Tuni C, Toft S, Bilde T. 2011. Worthless donations: Male deception and female counter play in a nuptial gift-giving spider. *BMC Evolutionary Biology* 11: 329.

Albrecht J, Hagge J, Schabo DG, Schaefer HM, Farwig N. 2018. Reward regulation in plant–frugivore networks requires only weak cues. *Nature Communications* 9: 4838.

Amato KR, Mallott EK, D'Almeida Maia P, Savo Sardaro ML. 2021. Predigestion as an evolutionary impetus for human use of fermented food. *Current Anthropology* 62: S207–S219.

Anderson JT, Saldaña Rojas J, Flecker AS. 2009. High-quality seed dispersal by fruit-eating fishes in Amazonian floodplain habitats. *Oecologia* 161: 279–290.

Araujo J, Correa S, Anderson J, Penha J. 2020. Fruit preferences by fishes in a Neotropical floodplain. *Biotropica* 1131–1141, 52.

Barlow C. 2008. *The Ghosts of Evolution: Nonsensical Fruit, Missing Partners, and Other Ecological Anachronisms*. Basic Books.

Barnhart MC, Haag WR, Roston WN. 2008. Adaptations to host infection and larval parasitism in Unionoida. *Journal of the North American Benthological Society* 27: 370–394.

Beasley DE, Koltz AM, Lambert JE, Fierer N, Dunn RR. 2015. The evolution of stomach acidity and its relevance to the human microbiome. *PLOS ONE* 10: e0134116.

Beerwinkle KR, Shaver TN, Lopez JD. 1993. Field observations of adult emergence and feeding behavior of *Helicoverpa zea* (Lepidoptera: Noctuidae) on dallisgrass ergot honeydew. *Environmental Entomology* 22: 554–558.

Bennett KF, Ellison AM. 2009. Nectar, not colour, may lure insects to their death. *Biology Letters* 5: 469–472.

Biben M. 1979. Predation and predatory play behaviour of domestic cats. *Animal Behaviour* 27: 81–94.

Boggs CL. 1995. *Male Nuptial Gifts: Phenotypic Consequences and Evolutionary Implications. Pages 215–242 in Leather SR, ed. Insect Reproduction*. CRC Press.

Bolmgren K, Eriksson O. 2010. Seed mass and the evolution of fleshy fruits in angiosperms. *Oikos* 119: 707–718.

Borchert M, Davis F, Kreitler J. 2008. Carnivore use of an avocado orchard in southern California. *California Fish and Game* 94: 61–74.

Borges RM. 2015. Fruit and seed volatiles: Multiple stage settings, actors, and props in an evolutionary play. *Journal of the Indian Institute of Science* 95: 93–104.

Brum D, Costa-Schmidt L, Araújo A. 2012. It is a matter of taste: Chemical signals mediate nuptial gift acceptance in a neotropical spider. *Behavioral Ecology* 23: 442–447.

Cipollini ML, Levey DJ. 1997: Secondary metabolites of fleshy vertebrate-dispersed fruits: Adaptive hypotheses and implications for seed dispersal. *American Naturalist* 150: 346–372.

Claus R, HO H, Karg H. 1981. The secret of truffles: A steroidal pheromone? *Experientia* 37: 1178–1179.

Cockburn G, Ko M-C, Sadanandan KR, Miller ET, Nakagita T, Monte A, Cho S, Roura E, Toda Y, Baldwin MW. 2022. Synergism, bifunctionality, and the evolution of a gradual sensory trade-off in hummingbird taste receptors. *Molecular Biology and Evolution* 39: msab367.

Correa S, Winemiller SB, López-Fernández H, Galetti H, Galetti M. 2007. Evolutionary perspectives on seed consumption and dispersal by fishes. *BioScience* 57: 748–756.

Correa SB, Oliveira PCd, Da Cunha CN, Penha J, Anderson JT. 2017. Water and fish select for fleshy fruits in tropical wetland forests. *Biotropica* 50: 312–318.

Cramer JF, Miller ET, Ko M-C, Liang Q, Cockburn G, Nakagita T, Cardinale M, Fusani L, Toda Y, Baldwin MW. 2022. A single residue confers selective loss of sugar sensing in wrynecks. *Current Biology* 32: 4270–4278.

Crockford C, Wittig RM, Langergraber K, Ziegler TE, Zuberbühler K, Deschner T. 2013. Urinary oxytocin and social bonding in related and unrelated wild chimpanzees. *Proceedings of the Royal Society B* 280: 20122765.

Crozier A, Clifford M, Ashihara H. 2006. *Plant Secondary Metabolites: Occurrence, Structure and Role in the Human Diet*. Blackwell.