Received: 17 November 2021 | Revised: 6 September 2022 | Accepted: 23 October 2022

DOI: 10.1002/evan.21967

REVIEW ARTICLE

Evolutionary Anthropology
ISSUES, NEWS, AND REVIEWS
WILEY

The sensory ecology of primate food perception, revisited

Carrie C. Veilleux[1] | Nathaniel J. Dominy[2] | Amanda D. Melin[3,4,5]

[1]Department of Anatomy, Midwestern University, Glendale, Arizona, USA

[2]Department of Anthropology, Dartmouth College, Hanover, New Hampshire, USA

[3]Department of Anthropology and Archaeology, University of Calgary, Calgary, Alberta, Canada

[4]Department of Medical Genetics, University of Calgary, Calgary, Alberta, Canada

[5]Alberta Children's Hospital Research Institute, University of Calgary, Calgary, Alberta, Canada

Correspondence

Carrie C. Veilleux, Department of Anatomy, Midwestern University, Glendale, AZ, USA.
Email: cveill@midwestern.edu

Amanda D. Melin, Department of Anthropology and Archaeology, University of Calgary, Calgary, AB T2N ON4, Canada.
Email: amanda.melin@ucalgary.ca

Funding information

National Science and Engineering Research Council (NSERC) Discovery Grant, Grant/Award Number: RGPIN-2017-03782; Canada Research Chairs, Grant/Award Number: 950-231257

Abstract

Twenty years ago, Dominy and colleagues published "The sensory ecology of primate food perception," an impactful review that brought new perspectives to understanding primate foraging adaptations. Their review synthesized information on primate senses and explored how senses informed feeding behavior. Research on primate sensory ecology has seen explosive growth in the last two decades. Here, we revisit this important topic, focusing on the numerous new discoveries and lines of innovative research. We begin by reviewing each of the five traditionally recognized senses involved in foraging: audition, olfaction, vision, touch, and taste. For each sense, we provide an overview of sensory function and comparative ecology, comment on the state of knowledge at the time of the original review, and highlight advancements and lingering gaps in knowledge. Next, we provide an outline for creative, multidisciplinary, and innovative future research programs that we anticipate will generate exciting new discoveries in the next two decades.

KEYWORDS

feeding, foraging, perception, primate evolution, sensation

1 | INTRODUCTION

Sensory systems play critical roles in all aspects of daily life, including mate selection, avoiding predators, and finding food.[1–4] During foraging, primates engage and integrate their senses throughout multiple stages of food detection and assessment.[5–7] However, much remains unknown about food sensory cues and signals, and about primate sensory morphology, genetics and behaviors. In the pages of this journal, Dominy et al.[5] published "The Sensory Ecology of Primate Food Perception." The authors noted that most studies of primate foraging at that time focused on nutritional ecology, and argued that it was necessary to establish a sensory link to nutrients. Dominy et al. provided a thorough review and ideas for future directions, with which they sought to stimulate additional research taking a sensory perspective. In this, the authors were highly successful; the study of primate sensory ecology has advanced significantly in the last two decades, propelled forward in part by advances from long-term behavioral research programs, and from the study of sensory systems and their underlying genetic basis. Recent research has also featured dozens of additional species, and brings insights from captive and wild settings using experimental and observational approaches.[8] Yet, there still remains large gaps in our understanding of primate sensory ecology. The time is therefore ripe for a review of progress in the last two decades, as well as a critical reflection on current gaps and opportunities for future research.

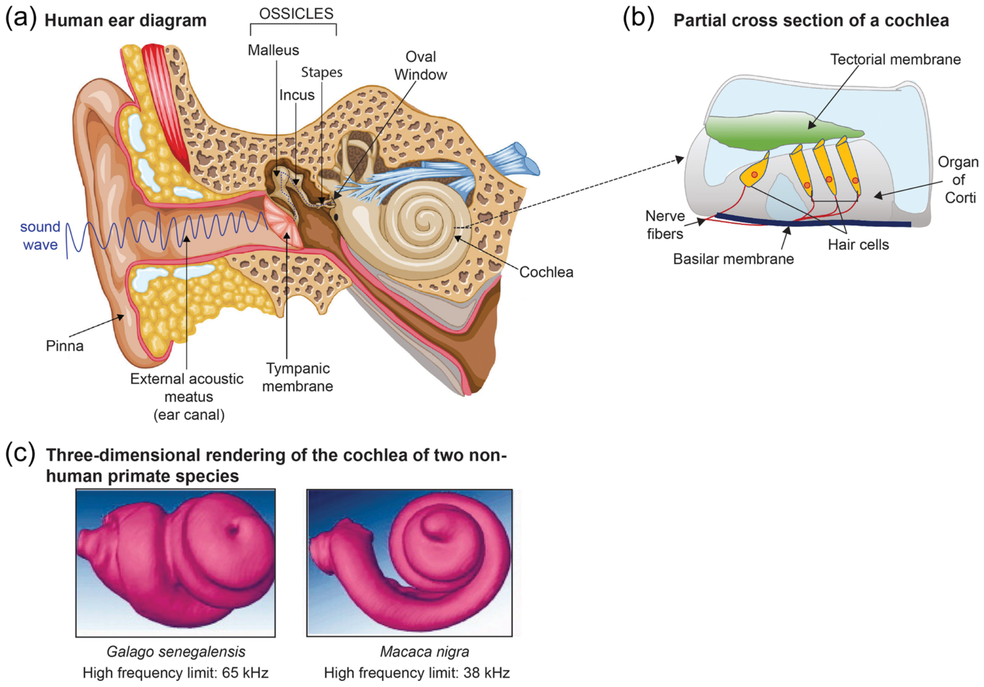
With these goals in mind, we review the current state the current state of primate sensory ecology research. For each sense, we begin with a high-level overview of sensory function, anatomy, physiology, and genetics. Our intention is to provide a quick primer that may be of interest to students or researchers new to the area. We then examine the behavioral ecology of each sense during foraging, providing examples to compare and contrast patterns across the Order. For each sense, we reflect on the state of knowledge in the original review, and highlight advances that have emerged since 2001. In the final section, we outline several areas that hold promise for advancing the discipline, including, ideas for creative, multidisciplinary research programs that will generate new discoveries, as well as highlight some important caveats with respect to primate sensory systems. Overall, we aim to provide a state-of-the-art summary of primate sensory ecology, to celebrate the achievements in primate sensory ecology that have recently emerged, and to inspire future innovative and integrative research that seeks to understand how primates use hearing, vision, touch, taste, and smell to navigate their environments.

2 | OVERVIEW OF CURRENT KNOWLEDGE

2.1 | Hearing

2.1.1 | Anatomy, physiology, and genetics

Audition is one of two mechanical senses, that is, signal propagation is initiated via physical distortion of sensory tissues. It begins when sound waves are funneled into the ear canal by the external pinnae. Some primates, including the strepsirrhines (lemurs and lorises) and the descendants of an early branch of the haplorhines, tarsiers (genus *Tarsius/Carlito*), have retained the ability to move their relatively large pinnae and an improved ability to localize sounds.[9,10] Mobile external pinnae were subsequently lost in haplorhine evolution, and are not found in platyrrhines (monkeys in the Americas) or catarrhines (monkeys and apes in Africa and Asia).[9,11] After entering the ear, sound waves travel through the tympanic membrane to the bones of the middle ear (auditory ossicles), which transmit and amplify the sound waves to the fluid-filled cochlea of the inner ear, causing the fluid to move mechanosensitive hair cells that convert the vibrations into electrical impulses (Figure 1a,b). Variation in the size and shape of these anatomical structures can affect the sensitivity of primate auditory systems to different auditory frequencies (Figure 1c).[9,12,14] For example, primate cochlear volume is negatively correlated with low- and high-frequency hearing limits.[12] Overall, primates are comparable to other similarly sized mammals in high-frequency hearing and exhibit reasonable sensitivity to low-frequency sounds.[10,15] However, the auditory sensitivities of primates can vary widely, sometimes as a function of phylogeny and head-size constraints,[10,16] or the pressures of natural and sexual selection.[17–19]



Galago senegalensis
High frequency limit: 65 kHz

Macaca nigra
High frequency limit: 38 kHz

FIGURE 1 (a) Sound waves are funneled into the external acoustic meatus by the pinna and cause the tympanic membrane to vibrate. This vibration is transmitted (dashed blue line) through the three ear ossicles (the malleus, incus, stapes) to the oval window on the cochlea. (b) Inside the cochlea, vibrations from the oval window create waves in the cochlear fluid and cause vibrations along the basilar membrane, which runs from the cochlear base to the cochlear apex. Attached to the basilar membrane is the Organ of Corti, which houses mechanosensitive hair cells. As the basilar membrane vibrates, these hair cells shear against the tectorial membrane and transduce the mechanical deformation into electrical stimuli. (c) In mammals, basilar membrane length and cochlear volume are associated with hearing frequency limits, even controlling for body size.[12] For example, galagos (*Galago senegalensis*) have a shorter basilar membrane, smaller cochlear volume, and an increased high-frequency limit compared to macaques (*Macaca nigra*). Human ear diagram reproduced from Stangor and Walinga[13] (https://opentextbc.ca/introductiontopsychology/wp-content/uploads/sites/9/2013/11/f13cbe628a50a1cd3243c0c1013450a1.jpg) and licensed by creative communications.org: https://creativecommons.org/licenses/by/4.0/. Three-dimensional cochlea renderings reprinted from Kirk and Gosselini-Ildari[12] with permission.

The genetic basis of auditory perception was poorly understood and not addressed in Dominy et al.'s[5] original 2001 review. Since then, at least 70 genes have been identified in humans as underlying the auditory sense,[20] but unfortunately, comparative study of the genetic basis of audition in nonhuman primates and other mammals remains almost nonexistent. A rare exception is recent work by Bankoff et al.,[21] who compared seven genes involved in auditory processing across echolocating mammals (bats, cetaceans) and primates to study the molecular evolution of specialized hearing in aye-ayes (*Daubentonia madagascariensis*). Aye-ayes use a derived percussive foraging technique that utilizes hearing to locate hollow cavities caused by wood-boring invertebrates,[21,22] and exhibit enhanced sensitivity to high frequencies relative to other strepsirrhines.[18] However, they found no evidence of convergent evolution between echolocating mammals and aye-ayes.

2.1.2 | Comparative sensory ecology

Hearing is a far-reaching sense, given the long propagations distances of some sound waves.[5,23,24] Dominy et al.'s[5] original publication reviewed the scant evidence for acoustic cues of food sites over long distances, highlighting how the calls of conspecific and heterospecific foragers, as well as the noises generated by food items themselves, may attract foragers. The state of the field has grown slightly since this time. For example, the pant hoots of chimpanzees (*Pan troglodytes*) can be heard from distances up to 1 km in some forests, and convey information about the quality of food patches.[25,26] Fruit-sourced noises themselves may also be informative. For example, at our study site in Costa Rica, some fruits (e.g., *Genipa americana*) make a resonating thud as they drop to the forest floor, which is audible to humans at distances beyond visual range (>30 m; A. Melin, pers. obs). However, putative auditory cues associated with fruits have received scant attention to date. A study of the acoustic properties of muskmelons when tapped (reported in Dominy et al.'s original review) remains one of the few detailed studies suggesting informative acoustic cues of fruit quality.[27] On the other hand, the last two decades have seen exciting discoveries in acoustic foraging for prey, especially among nocturnal primates.[22,28] Aye-ayes rely on soft prey cues during tap-scanning for embedded invertebrate prey[22] and experiments on mouse lemurs (*Microcebus murinus*) reveal that soft prey noises in isolation from other sensory cues are sufficient to lead to prey capture.[28] Importantly, prey movement generates both visual and auditory cues simultaneously, creating potential for multimodal signaling. Primates may respond accordingly with multiple sensory systems in the "visual orienting reflex," where "the ears tell the eyes where to look." That visual and hearing acuity are correlated in small insectivorous mammals, lends support to a hypothesis that these two systems have a coordinated evolution in some species.[10]

Whether the foods are vegetative or animal in nature, the dynamic detection range of acoustic cues is determined by the amplitude and frequencies of the sound, the properties of the environment, the presence and overlap of ambient (background) acoustic noise, and by the sensitivity of receiver auditory systems.[23,29] Higher frequency sounds, for example, attenuate relatively quickly, and their attenuation is affected by environmental and climatic conditions including the canopy height of the sound source, foliage density, temperature, and humidity.[23,30] Naturally, the perception of ambient noises is determined not only by the environment, and distance to the source, but by the sensitivity of the receiver's auditory system. There is growing recognition of the dynamism and intra- and interspecific variation in primate audition.[15] For example, both slow lorises and tarsiers are now known to use ultrasonic communication, detecting noises completely imperceptible to humans and other sympatric primates.[17,31] Yet, despite the important roles the sense of hearing plays in primate foraging ecology, and recent advances in the last 20 years, it remains an understudied topic with considerable promise for future study.[15,18,24,31]

2.2 | Olfaction

2.2.1 | Anatomy, physiology, and genetics

Volatile and semivolatile compounds (odors) are perceived through the main olfactory system when they bind to and stimulate the olfactory receptors expressed in the olfactory epithelium, lying under the cribriform plate of the turbinate bones of the nose. From here the olfactory receptor neuronal axons travel to the olfactory bulb of the brain to be integrated with other sensory information for downstream neural processing (Figure 2).[33] Many primates also possess a vomeronasal organ that is used during social communication.[32,34,35] This system is prominent in strepsirrhines, variable in platyrrhines, and largely absent in catarrhines. While new discoveries in vomeronasal-mediated social behaviors are emerging, given the focus of our review, we concentrate on the main olfactory system due to its prominent role during primate foraging.

Study of primate olfaction was in its infancy in 2001, and olfaction as a "neglected sense" was highlighted in a special issue of the *American Journal of Primatology* in 2006.[36] We have seen considerable advances in the past two decades. Primates have traditionally been characterized as "microsmatic" (e.g., having a poor sense of smell) relative to other mammals. However, research now suggests that this characterization is overly simplistic.[37–39] While there is evidence of reduction in smell in haplorhines compared to other mammals (characterized by loss of intact olfactory receptor genes[37] and reduction in olfactory bulb volumes[38]), analyses of other structures, such as nasal epithelia,[39] are more equivocal. Primate olfactory epithelia are estimated to house hundreds of olfactory receptors and to be sensitive to a huge range of odorants.[40] For example, it is estimated that humans can sense >1 trillion odors.[41] Moreover, these studies suggest that strepsirrhines have retained a strong sense of smell and may be derived in some aspects of olfaction compared to crown primates.[37,38]

The dynamics of olfaction are complex, and we still have a poor map of which compounds stimulate which receptors, or the breadth

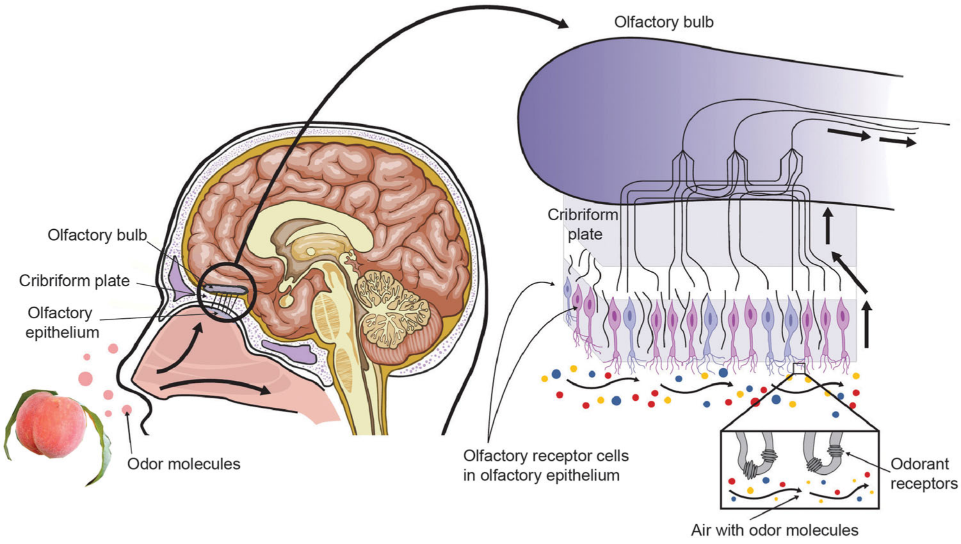


FIGURE 2 Odor transmission, from the olfactory epithelium to the brain. Odor molecules bind to olfactory receptor cells in the olfactory epithelium of the nasal cavity. These olfactory receptor cells transduce chemical stimuli into electrical stimuli and transmit the information to the olfactory bulb of the brain via olfactory nerves that run through foramina in the bony cribriform plate of the ethmoid bone. The absolute area of the cribriform plate is associated with the number of functional olfactory receptor genes across mammals.[32] The information is then transmitted from the olfactory bulb to higher processing regions of the brain. Figure modified from Stangor and Walinga[13] (https://opentextbc.ca/introductiontopsychology/wp-content/uploads/sites/9/2013/11/8160ad1108b8ba82ab80260f3e7b5161.jpg) and licensed by creative communications.org: https://creativecommons.org/licenses/by/4.0/

and sensitivity of their responses.[42] Furthermore, olfactory receptors have complex "many-to-many" relationships with sensory stimuli, meaning that one receptor can respond to many compounds and one compound can trigger many receptors, which complicates our understanding of olfactory function and evolution. Given the large number of olfactory receptors, it is unsurprising that olfactory receptor (*OR*) genes represent one of the largest gene families in mammals. *OR*s are known for their rapid evolution, including high rates of gene duplications and losses, which makes analyses of their evolution and function a technical challenge.[43] However, knowledge of olfactory genomics is growing rapidly, facilitated by the large throughput capacity and comparative power of recent genomic methods coupled with assays of genes expressed in vitro.[42,44] For example, a comparative analysis of intact *OR* genes across 50 mammalian species provides compelling data that ecotype (aquatic, semiaquatic, terrestrial, flying) shapes olfactory evolution.[45] Additionally, the same *OR* genes can respond to the same ligand with very different efficacy even among closely related species.[38,42,43]

2.2.2 | Comparative sensory ecology

In 2001, our knowledge of how, when, and why primates used their sense of smell to find and assess foods was limited.[5,36] Now we are pleased to report there has been an upswing in the number of studies on primate olfaction and increasing appreciation of its importance.[28,46,47] These studies have been facilitated in part by improvements in the technology for sampling, storing, and analyzing volatile organic compounds (VOCs) under field conditions.[48–50] For example, Dominy et al. reported anecdotal evidence and a personal communication that marmosets scent-mark feeding sites. Recent studies provide direct behavioral evidence of this behavior and report the VOC composition of marmoset scent marks deposited at feeding sites and of dietary exudates.[51,52]

Field studies have also revealed that many primates frequently sniff fruits before ingestion or rejection.[7,53,54] Experimental work upholds the importance of olfaction in both strepsirrhine and haplorhine primates. Squirrel monkeys (*Saimiri sciureus*) and pig-tailed macaques (*Macaca nemestrina*), for example, are sensitive to extremely low concentrations of fruit-associated esters, aldehydes, and alcohols, that cannot be detected by other mammals, such as dogs and rats, known for their good sense of smell.[55] Both ring-tailed lemurs (*Lemur catta*) and humans can track odor plumes.[56,57] Interestingly, capuchin monkeys (*Cebus imitator*) and spider monkeys (*Ateles geoffroyi*) sniff visually "cryptic" (ever-greenish) or unripe fruits more often than fruits undergoing that change color as they ripen,[58,59] suggesting increased olfactory reliance when visual ripeness cues are less salient. These results may offer insight into the fruit syndrome hypothesis, which predicts that the evolution of fruit traits are correlated (specifically due to selective pressures exerted by seed dispersers). One prediction of this hypothesis is that visually "cryptic" fruits may produce a stronger odor signal, while more colorful fruits have less of an odor change with ripeness.[43,47,60–63] The difference in primate olfactory behaviors used to assess fruits of different color conspicuity lend support to this idea.

Inorganic volatiles may also play an important, but underexplored role in food selection, or aversion. For example, inorganic volatiles that are perceived and typically elicit disgust reactions among humans include hydrogen sulfide (a smell associated with foul eggs) and ammonia, which are released from microbial breakdown and decomposition of animal and plant products.[64,65] Our sensitivity to these molecules is likely to be adaptive, perhaps in avoiding of potentially hazardous organic matter during foraging and feeding. While the odorants were not examined, Case et al.[66] recently summarized clear cases of chimpanzees and other primates tasting and smelling food objects, such as rotting plant material and meat, and fecal-contaminated foods, and then showing a strong aversive reaction. Such findings invite further research on the potential role of inorganic compounds in mediating food perception.

Primates vary substantially in their olfactory ecology, which has been shaped by their evolutionary histories and dietary strategies.[32,37,67] In particular, the dynamics of odor plumes may be important. These are dependent on many environmental factors, including vegetation density, barometric pressure, temperature, humidity, and air currents.[68] Consequently, the salience of odor cues for foraging likely varies across primates with habitat use and activity pattern. Habitat effects on primate olfaction have yet to be explored, although the "odorscape" is a growing research topic in sensory ecology[69,70] (see also Section 3.5). While experimental work suggests that nocturnal strepsirrhines and platyrrhines use olfaction to forage for fruit and insects,[28,71] comparative studies have been equivocal.[37,67,72] For example, the number of functional *OR* genes is similar among nocturnal and diurnal species[37] despite substantial differences in olfactory bulb volume.[67] Dietary specialization has also been found to influence the degree of reliance on olfaction. Frugivorous species tend to exhibit increased olfactory reliance (measured behaviorally, anatomically, and genetically) relative to other primates. Spider monkeys (*A. geoffroyi*) use olfaction during fruit investigative behaviors significantly more often than sympatric species[7] and are more likely to use olfaction to investigate novel food objects.[73] Recently, Nevo et al.[74] demonstrated that spider monkeys can also discern between the odors of unripe versus ripe fruits. The overall odor plume, rather than the amount of any specific compound, was particularly important in odor discernment.[74] Similarly, frugivorous lemurs (*Varecia variegata*) were more efficient than folivorous (*Propithecus coquereli*) or generalist (*L. catta*) taxa at using odor cues to select higher quality foods in a captive experiment.[75] Frugivorous primates tend to have larger *OR* gene repertoires[37] and larger olfactory bulbs.[67] The impact of local environments and diets have also been implicated in shaping *OR*s in modern and extinct *Homo*.[44,76]

2.3 | Vision

2.3.1 | Anatomy, physiology, and genetics

A defining characteristic of Primates is its increased emphasis on vision relative to other mammals.[77] It is perhaps unsurprising that vision is the most studied sense in primate sensory ecology. Research over the last 20 years has greatly increased our understanding of the diversity of primate visual function, anatomy, and genetics, documenting dramatic variation across species often correlated with ecology.[78–82] For example, primates vary in substantially in visual acuity (i.e., the ability to resolve fine details, Figure 3, Box 1), with values ranging from 2.8 to 7 cycles per degree (cpd) in strepsirrhines,

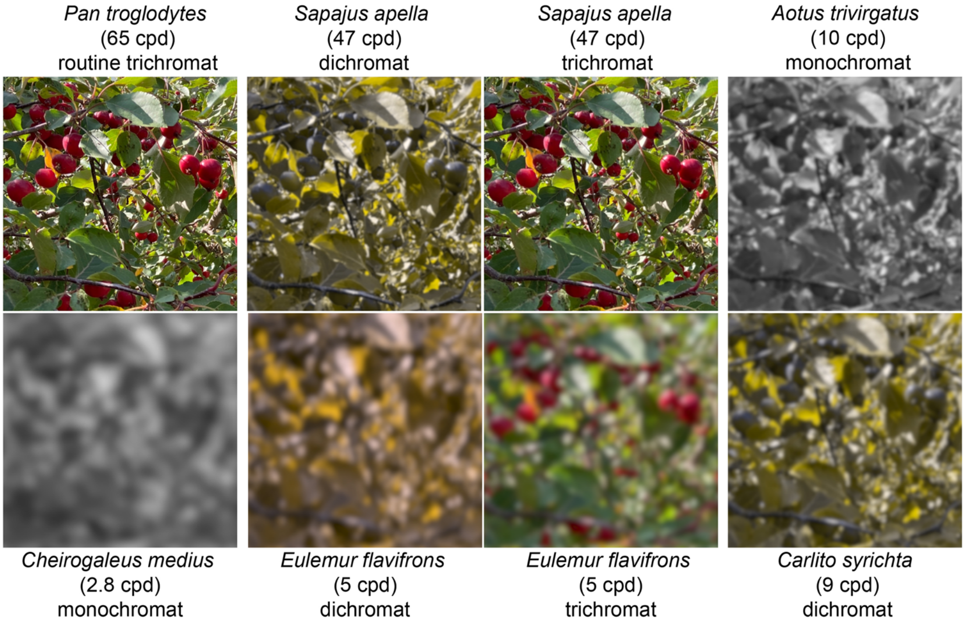


FIGURE 3 Modeled variation in primate color vision and acuity, comparing how small (2-cm) fruits are perceived from 2 m by representative taxa. Visual acuity is measured in cycles per degree (cpd), referring to the number of distinct lines that can be discriminated in one degree of visual angle. Catarrhines such as *Pan* exhibit high visual acuity and routine trichromacy. All diurnal platyrrhines have high visual acuity and either routine trichromacy or allelic trichromacy (e.g., *Sapajus apella*). Nocturnal haplorhines exhibit lower acuity relative to diurnal taxa, and are either dichromats (e.g., *Carlito syrichta*) or monochromats (e.g., *Aotus trivirgatus*). Strepsirrhines have lower acuity in general, and exhibit monochromacy (e.g., nocturnal *Cheirogaleus medius*), dichromacy, or allelic trichromacy (e.g., cathemeral *Eulemur flavifrons*). Images created using AcuityView.[83] Original photograph of crab apple fruit (genus *Malus*) by A. Melin.

BOX 1. Definitions of sensory modalities

In our review of literature over the past two decades, it has become clear that there is a lack of consistency and clarity in the language used to describe the senses. For example, it is not uncommon to see broad claims like "folivory is associated with reduced importance of olfaction," or "acuity" and "sensitivity" being used interchangeably, particularly when referring to nonvisual senses. We propose a movement toward greater precision of language in primate sensory ecology (Table 1). Psychophysics can offer a starting point, with already present terminology differentiating functional modalities.[84,85] Evidence suggests modalities within a sense can have different anatomical correlates—a recent imaging study in humans,[86] for example, suggests that different olfactory functions (threshold detection, discrimination, and identification) are associated with distinct divisions of the olfactory system (olfactory bulb volume, orbitofrontal cortex volume). Using the visual modalities as a guide, we propose the following three broad modalities for sensory function: resolution, sensitivity, and breadth. We suggest united terminology across senses for each of these functional modalities. The suggestions in Table 1 are not perfect, and there is often overlap between categories. Audibility threshold, for example, varies with spectral frequency. Table 1 does, however, offer a starting point for clarifying our language when describing correlations between aspects of sensory anatomy/genetics and sensory function.

TABLE 1 Proposed modalities of sensory function, terminology, and examples of data

	Resolution **At what level can you distinguish two stimuli as distinct?**	**Sensitivity** **At what level can you detect a stimulus as present?**	**Breadth** **How many different types of stimuli can you detect?**
Vision	Spatial acuity *cycles per degree*	Visual sensitivity *thresholds of cone and rod function*	Color vision *Number of distinct colors* *(e.g., diversity of opsin genes)*
Olfaction	Olfactory acuity *accuracy of odor identification*	Olfactory sensitivity *detection threshold* *(e.g., concentration of odorant)*	Olfactory breadth *number of distinct odors* *(e.g., size of OR gene repertoire)*
Hearing	Temporal resolution *Detect two tones as separate in time* Pitch perception *Detecting spectral frequencies as distinct*	Audibility threshold *Lowest sound pressure needed to detect a spectral frequency*	Frequency range *number of different spectral frequencies* *(e.g., upper and lower limits of spectral frequencies that can be perceived)*
Touch	Spatial acuity *detect two points on skin as separate* *(e.g., two-point touch threshold)*	Tactile sensitivity *pressure threshold, vibratory threshold*	Tactile breadth *different textures and vibration frequencies* *(e.g., diversity of different types of mechanoreceptors)*
Taste	Taste resolution *distinguish between concentrations of same tastant*	Taste sensitivity *detection threshold* *(e.g., concentration of tastant)*	Taste breadth *number of different tastants (e.g., diversity of functional taste receptor genes)*

~9 cpd in tarsiers and owl monkeys, and up to 25–64 cpd (or 20/40 to 20/20 vision) in diurnal haplorhines.[79,87] Monkeys and apes exhibit extensive anatomical features that support high acuity (e.g., postorbital closure, cone-dense retinal fovea, lower retinal summation of cones[88]). These adaptations are consistent with a large comparative study of mammal acuity[79] which found that diurnal haplorhines have significantly higher acuity than other mammals, even after controlling for their large eye size.

Color vision, referring to the ability to discriminate between wavelengths of light (Box 1), is particularly interesting due to its derived state in primates, and the high levels of intra- and interspecific variation. Most mammals possess two cone types, one short-wavelength-sensitive (SWS) cone type and one medium/long-wavelength-sensitive (M/LWS) cone type, sensitive to shorter and longer wavelengths of light, respectively.[89] Primates are unique among placental mammals in having evolved trichromatic color vision via variation and/or duplication and divergence of the *OPN1LW* gene, leading to separate MWS and LWS cones and the ability to discriminate among greens, yellows, oranges, and reds. Although the basic biology of primate color vision diversity was well known before the original 2001 review, the last 20 years has seen an explosion of studies investigating opsin genes and color vision across most primate clades. Dominy et al.[5] offered hypotheses of the ecological value of trichromacy that were largely untested at the time, including the relatively new hypothesis that trichromacy could be an adaptation for folivory. Hundreds of new studies published since 2001 have greatly expanded our understanding of the variability of primate color vision, as well as providing new insights into the history of selection pressure acting on color vision in different clades. We summarize some of these below (also see Moreira et al.[90] for a recent review).

Recent studies of opsin genes have revealed that the evolution of color vision has varied remarkably between and within primate clades. Catarrhines share uniform routine trichromacy, wherein a gene duplication led to distinct *OPN1MW* and *OPN1LW* genes producing separate MWS and LWS cones in all individuals.[89] In general, catarrhines have experienced strong purifying selection to maintain trichromacy and exhibit a low incidence of color vision defects.[91–93] The ratio of LWS to MWS cones in the retinas of catarrhines also seems relatively consistent, with an average of 1:1.[94,95] Humans are an exception, with high levels of genetic variation in the *OPN1MW* and *OPN1LW* genes and variable cone ratios, both leading to highly variable color vision.[94,96] Color vision in platyrrhines is also highly variable, however, for different reasons (Figure 3); owl monkeys (genus *Aotus*) have lost functionality in the *OPN1SW* opsin gene and cone-based color vision. Howler monkeys (genus *Alouatta*) independently evolved routine trichromacy, and all other platyrrhine taxa exhibit allelic trichromacy, also known as polymorphic trichromacy or polymorphic color vision.[89] In the latter condition, polymorphism of the X-linked *OPN1LW* gene results in mixed populations of dichromatic (homozygous females and hemizygous males) and trichromatic (heterozygous females) individuals. The number of different *OPN1LW* alleles producing functionally distinct M/LWS cones varies across platyrrhine species, with some taxa possessing only two alleles, and others up to six.[97–99] In contrast, among the strepsirrhines, all lorisiforms have lost SWS cones entirely due to shared deleterious mutations in the *OPN1SW* gene.[100] Some of the most exciting research in the last 20 years has revealed surprising variability in the color vision of lemurs. While many nocturnal species retain dichromacy, SWS cone loss has occurred multiple times in the Cheirogaleidae family, including in dwarf lemurs (genera *Cheirogaleus* and *Allocebus*) and fork-marked lemurs (genus *Phaner*), and there is variation in selective constraint on *OPN1SW* between species within other nocturnal genera.[81] Moreover, although some diurnal and cathemeral taxa are dichromats, others exhibit allelic trichromacy (genera *Eulemur*, *Propithecus*, *Varecia*, *Indri*).[82,101,102] Recent work has identified variation in the number and spectral tuning of *OPN1LW* alleles across taxa, even among congeners.[82,103,104]

2.3.2 | Comparative sensory ecology

Vision is important in both long-range detection of foods and short-range evaluation of food quality. In general, the visual range of food detection is limited by the size of the target, the light environment, obstacles in the environment, and the visual acuity of the primate species (Figure 3). In cluttered forested habitats, diurnal visibility is typically less than 20–30 m.[5] Detection of foods using chromatic cues depends upon the spectral reflectance of the food, the color vision and acuity of the receiver, and the light environment.[105] In 2001, Dominy et al. called for observer-objective measures in the study of color and color vision. Happily, the standard for color vision research over the last 20 years indeed includes spectroscopy or standardized digital photography to obtain objective reflectance spectra, quantum-catch models to consider species-specific visual spaces, and measurement of natural environments with sensitive spectroradiometers.[106–109] While the colors of light in diurnal terrestrial habitats has been extensively documented since the 1990s,[110] the last 20 years has seen the addition of light spectra for primate-inhabited forests at night and twilight (Figure 4),[112,114] facilitating studies on the use of vision, especially color vision, by night active primates.[48,87,104,115,116]

During foraging, primates use vision to detect pattern, shape, size, movement, depth, luminance (brightness) contrast, and chromatic (hue and saturation) cues. Research over the last 20 years suggests that the most salient cues likely vary with foraging strategy. Faunivores, for example, may prioritize detecting movement, shape, depth, and luminance contrast to aid in detecting, tracking, and capturing small, visually cryptic prey. These cues also aid in detecting camouflaged invertebrates against matching backgrounds.[117] Dichromats are better than trichromatic conspecifics in capturing cryptic insects, likely due to a heightened ability to perceive borders, textures, and shapes when avoiding "chromatic" noise.[118–120] Faunivorous primates and mammals also exhibit higher orbital convergence and higher visual acuity relative to herbivorous taxa.[78,79] In contrast, chromatic, size, and luminance cues are likely more informative to primates feeding on fruits, flowers, or young leaves. For these foods, color can aid primates in detecting food patches against the background foliage.[5,102,121–123] Moreover, color can sometimes provide a signal of food quality. In leaves, variation in chromatic channels is significantly correlated with protein content, toughness, and phenolic content.[124] In fruits, color can be linked to sugar content,[125] although several studies from forests around the world (Costa Rica, Uganda, Madagascar, Singapore) suggest that color is often not a reliable cue for such measures of nutritional ripeness in some plant species, including sugar content.[53,54,126] In these species, color change may precede nutritional ripeness, and other sensory cues are also needed once the patch of potentially ripe fruit is located.

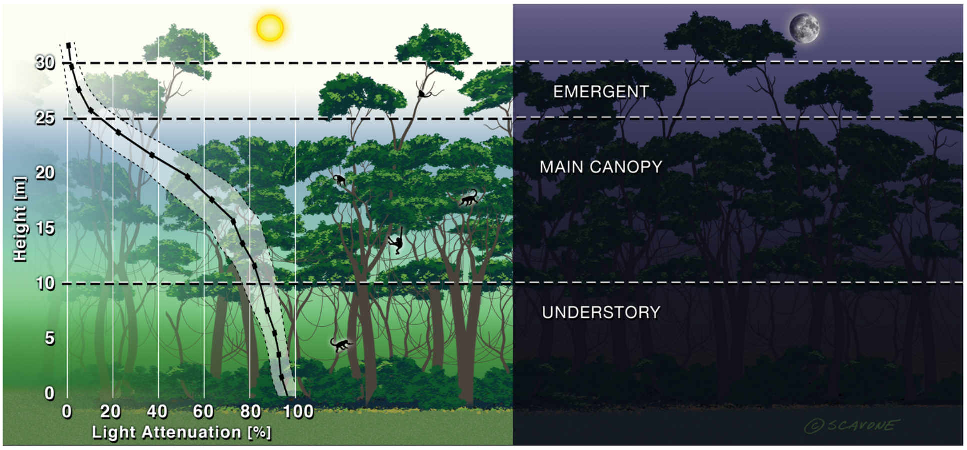


FIGURE 4 Vertical variation in the intensity and color of downwelling light in a tropical rainforest. Mean attenuation of light intensity (solid black line) ±1 SD (dashed black lines) of 36 light transmission profiles in Rio Surumoni, Venezuela.[111] Similar levels of vertical light extinction are expected at night, but systematic data from primate habitats are scarce.[112] The color (spectral composition) of downwelling light also changes vertically,[110] from whitish ("open/cloudy") to bluish ("woodland shade") to greenish ("forest shade"). At night, the color of light in forests tends to resemble "forest shade," regardless of lunar phase or canopy openness.[112] Illustration by William Scavone, and reproduced from Dominy and Melin.[113]

Much of the research in primate visual ecology over the last two decades has focused on exploring the relative foraging benefits of trichromacy and dichromacy, centering around two major questions: (1) what ecological factors have led to the convergent evolution of routine trichromacy in catarrhines and in howler monkeys?; (2) why has allelic trichromacy been maintained in platyrrhines and lemurs? For the first question, studies of catarrhines and howler monkey foraging ecology have supported the hypothesis that routine trichromacy was favored to facilitate seasonal exploitation of young reddish leaves as fallback foods.[122,124,127] Howlers and catarrhines are large enough to subsist primarily or exclusively on leaves during periods of fruit dearth.[128] Because trichromacy is useful for both leaf and fruit detection and selection, the genetic fixation of gene duplications leading to routine trichromacy may have been ubiquitously favored.[122] Additionally, the strong visual reliance of both these primate lineages, as indicated by their high visual acuity,[79] may have also played a role. Regarding the second question, evidence from patterns of gene variation provides clear evidence of balancing selection maintaining opsin polymorphism.[129] In smaller bodied diurnal primates, selective pressures for efficient capture of invertebrates as fallback food and dietary supplements may have favored the persistence of dichromacy via a dichromatic advantage in detecting these cryptic foods,[118–120,122,130] but see Troscianko et al.[131] While early studies largely failed to detect a clear trichromatic advantage in fruit foraging,[121,132,133] more recent work from long-term field sites has found trichromat advantages for fruit and flower detection and feeding efficiency in both platyrrhines[123,134] and lemurs.[102] Yet, evidence from relative reproductive success in one well-studied population of capuchin monkeys argues against heterozygous advantage.[135] Thus, debate among other mechanisms of balancing selection continues,[136] without a clear resolution.

There has been a concerted focus over the last 20 years to expand our understanding of the visual ecology of nocturnal primates and low-light environments (e.g., lemurs,[28,81,114] lorisiforms,[87,137,138] tarsiers,[80,116,139] owl monkeys[140,141]). Prey capture using visual cues is possible in natural nocturnal light levels,[28] overturning ideas that vision is useless at night, and suggesting positive relationships between insect foraging and nocturnal light intensity.[139,142] Nocturnal primates also seem to employ chromatic cues when foraging on fruit, flowers, and leaves, similar to their diurnal counterparts.[48,112,114,115] Valenta et al.[48] found that the fruits dispersed by mouse lemurs (*M. murinus* and *Microcebus ravelobensis*) differed in blue-yellow contrasts relative to background leaves significantly more than nondispersed fruit. The importance of chromatic cues has been linked with selection to maintain dichromatic color vision in many nocturnal taxa.[81,114,115,143] In contrast, the loss of SWS cones and functional color vision in many nocturnal exudate feeders (e.g., *Phaner*, *Allocebus*, *Galago*) is hypothesized to be associated with a greater emphasis on luminance rather than chromatic cues,[87,144,145] as luminance contrast can be more useful in identifying gum resources, which often stain darkly against tree bark.[145] A linked and important advancement of the past two decades has been the recognition that "diurnal" and "nocturnal" light environments, and especially their transitional phases (e.g., twilight) are variable, dynamic, and influenced by habitat types, lunar cycles, and anthropogenic disturbance.[112–114,146] Data from behavioral study of foraging in dichromatic marmosets (*Callithrix jacchus*) indicates complex impacts of light levels on color perception due to input from rods under mesopic conditions[147]; such phenomena remain poorly understood. Overall, mesopic and liminal light environments likely had a profound and underappreciated impact on early primate sensory evolution and ecology, and are still important to many species.[113,140]

2.4 | Touch

2.4.1 | Anatomy, physiology, and genetics

Like audition, the sense of touch is a mechanical sense, where specialized receptors respond to nonpainful deformation of the skin.[148] While there are multiple types of touch, the one most relevant to primate feeding ecology is discriminative touch, referring to the ability to detect shapes, texture, vibration, and object movement. In primates, discriminative touch is focused in nonhairy "glabrous" skin (e.g., palms and fingers of the hand, soles, and toes of the feet, lips, and genitals) and in vibrissae (whiskers). There are four types of mechanoreceptors in glabrous skin, each responding to different types of stimuli (although these four submodalities interact to contribute to different aspects of tactile sensation).[149] Tactile epithelial (Merkel) cells respond to light pressure and detect object shape, edges, and texture, while tactile (Meissner) corpuscles are sensitive to low-frequency vibration and movement across the skin, such as fine-surface texture or object slippage.[148] Meanwhile, lamellar (Pacinian) corpuscles respond to high-frequency vibrations (>200 Hz), and bulbous (Ruffini) corpuscles respond to heavy touch, pressure, and stretching.[150] Variation in mechanoreceptor densities between anatomical regions (e.g., hand, foot) are associated with differences in tactile acuity for these different stimuli.[151,152] In humans, for example, fingertips have the highest mechanoreceptor density (particularly tactile corpuscles and tactile epithelial cells) and the highest tactile acuity as measured by the detection threshold for two-point discrimination.[151,153]

Researchers have only recently begun to identify genes involved in mechanoreceptor function. Many of these genes and proteins are associated with ion channels, in which mechanical pressure is transduced into electrical/chemical stimuli (e.g., *Piezo2*).[154–156] Experimental, clinical, and comparative work in humans and other vertebrates suggests that variation in both the gene sequence and the expression level of mechanoreceptor genes is associated with differences in tactile sensitivity and mechanoreceptor density.[154,156,157] Of particular interest to primate sensory ecology, animals that rely on tactile cues during foraging (ducks) exhibit higher levels of mechanoreceptor gene expression and larger trigeminal neurons than visually foraging taxa (chickens, pheasants).[156]

2.4.2 | Comparative sensory ecology

In contrast to audition, olfaction, and vision, the sense of touch is only involved in food perception at short range (e.g., arm's length or snout's length away). Touch can provide crucial information during foraging, particularly when foraging on fruit or other soft foods. Primates have been observed to use maxillary touch (e.g., lips, vibrissae) and manual (hand) touch in fruit evaluation.[7,53,54,59,103,158] In prehensile-tailed species, the tail can also be used for food retrieval and object manipulation.[159,160] For many fruit species, haptic cues such as elastic modulus (deformability) are more reliable indicators of nutritional ripeness than other sensory cues, including color.[54,59,126,161] Consequently, frugivores are predicted to exhibit greater tactile sensitivity in the face and hands relative to folivores (the "fruit texture hypothesis"[162]). However, sensitive discriminative touch is also likely closely associated with increased manual dexterity, given the need for sensory feedback in dexterous tasks.[54] Thus, touch is further hypothesized to play a role in insect capture[73,163] and manual tool use and extractive foraging.[164,165] While we focus here on maxillary, manual, and tail touch, we note that oral mechanosensation is also likely important in food assessment. Teeth contain mechanoreceptors that are involved in monitoring tooth load and can detect food texture during mastication,[166,167] while the tongue also is highly sensitive to touch.[168] The role of oral mechanosensation is currently unexplored in the context of primate feeding ecology.

Dominy et al. suggested in 2001 that "although the origin of skilled forelimb movements in vertebrates has been related to food-handling, relatively few studies have examined how primates use their hands for this behavior." Comparative research on primate touch has remained relatively scarce, and much of the work that has been performed has utilized anatomical proxies of touch. For example, frugivorous primates have significantly larger infraorbital foramina (which carries the nerve innervating maxillary mechanoreceptors of the upper lip and vibrissae) than folivorous or insectivorous taxa.[169] However, both omnivorous dwarf lemurs and aye-ayes also have very large infraorbital foramina, possibly associated with the prominent role played by vibrissae and anterior teeth during bark gouging.[163] In general, however, primates and other eurarchontans are characterized by a reduction in infraorbital foramen size compared to other mammals, possibly reflecting a shift in reliance from maxillary touch to manual touch.[170,171] This reduction in infraorbital foramen area is also observed in crown fossil primates (adapoids, omomyoids), but not plesiadapiforms.[171] Comparative studies of mechanoreceptor densities in primate hands are also limited but the available results have been equivocal. While Hoffmann et al.[162] found a positive correlation between the percent frugivory in the diet and the tactile corpuscle density in the fingertips, Verendeev et al.[172] found no relationship between tactile corpuscle density and frugivory or manual dexterity (although it must be noted that Verendeev et al.'s primate sample was >60% frugivorous). Mechanoreceptors do vary in the skin of the tail between prehensile- and nonprehensile-tailed monkeys.[150] The glabrous skin of the distal tail in spider and woolly monkeys (genera *Ateles* and *Lagothrix*, respectively) contained all four types of mechanoreceptors found in the hands.[150] In contrast, only tactile epithelial cells and bulbous corpuscles were found in the capuchin semiprehensile tail, and just bulbous corpuscles were present in the nonprehensile tail of the squirrel monkey (genus *Saimiri*). Behavioral data on interspecific variation in the use of touch is primarily descriptive for wild primates,[54] although there are limited data on variation among captive taxa.[73] In one of the only quantitative studies of touch behavior in wild primates, members of the present authorship recently compared the use of manual touch during foraging on the same fruits in three species of sympatric primates in Costa Rica (*C. imitator*, *A. geoffroyi*, *Alouatta palliata*). Melin et al.[7] found that more frugivorous species (*Cebus*, *Ateles*) used touch significantly more often than *Alouatta* when evaluating fruit, with *Cebus* using manual touch the most.

2.5 | Taste

2.5.1 | Anatomy, physiology, and genetics

The sense of taste joins olfaction as the second chemical sense, and is subdivided into five modalities that each play an important role in evaluating food quality and palatability: sweet (carbohydrate detector), bitter (toxin detector), sour (unripe/soiled detector), umami (protein detector), and salty.[173] More recent work has identified a sixth modality: fat taste ("oleogustus"), referring to the detection of long-chain fatty acids.[174] Receptors for these modalities are found in taste bud cells located in papillae along the surface of the tongue.[175] Over the last 20 years, there have been dramatic advances in our understanding of the molecular mechanisms of taste. Bitter, sweet, and umami receptors are encoded by two families of genes: *TAS1R*s (sweet and umami) and *TAS2R*s (bitter).[173,176] In general, primates exhibit comparable numbers of *TAS1R* and *TAS2R* genes compared to other mammals.[177,178] However, there is substantial variation in the sequences of these taste receptor genes both between and within primate species. Consequently, research in both human nutrition and primate sensory ecology have focused on exploring the relationships between this genetic variation and individual and species-specific taste sensitivities and food preferences.[179–182] The molecular mechanisms involved in the other taste modalities (salt, sour, fat), are relatively less well understood, but several candidate genes have been proposed in the last 10 years.[175,183,184] Further, contrary to popular belief of a "taste map" of the tongue (e.g., that parts of the tongue specialize in different taste modalities), all major taste modalities are expressed in all regions of the tongue.[176]

The last 20 years has also seen renewed interest in physiologically evaluating taste sensitivities to different compounds across primate species, particularly in relation to dietary strategy and body size. While much of this work began in the late 1990s and early 2000s with Hladik and colleagues,[185–187] the last two decades have seen tremendous growth. In one recent example, Pereira et al.,[188] used two-bottle tests to measure taste sensitivities to eight sweet compounds in spider monkeys (*A. geoffroyi*) and chimpanzees (*Pan troglodytes*). They identify substantial interspecific variation in sensitivity to the different compounds, which they suggest is due to co-evolution with different fruit-bearing plants. In another example, Toda et al.[189] examined amino acid variation and perception of "umami" taste across primates, linking shift to major diet transitions. Data have now been collected for many species, taste receptors, and compounds. The Institute for Neuroethology at the University of Veracruz, Mexico, Linköping University in Sweden, and the Primate Research Institute of Kyoto University, Japan, have been hotspots for this research, consistently leading the field in gustation research.[188,190–194]

2.5.2 | Comparative sensory ecology

Taste, occurring just before ingestion, is one of the last senses used during food evaluation. A number of studies have identified an important role for taste during food selection.[7,54,59,103,133] However, identifying the sensory basis for food rejection after biting during behavioral observations can be challenging, given the multiple types of sensory cues available with biting, including taste or oral mechanosensation.[7] It is also important to consider primate taste in the context of a co-evolutionary relationship with plants. Leaves and bark often contain distasteful bitter compounds to deter feeding, while nectar and fruit often contain high-calorie sugar rewards to encourage pollination and seed dispersal, respectively. Interestingly, some plant species cheat by producing fruit with "sugar mimics" that are made of low-calorie proteins rather than high-calorie sugars, and primate species vary in whether they perceive these sugar mimics as sweet, suggesting an ongoing "arms race" between primate frugivores and fruiting plants.[195]

Not surprisingly, different aspects of primate taste (Box 1) appear to be associated with feeding strategy. Frugivorous and nectarivorous primates, for example, are highly sensitive to sugars found in fruit and nectar, for example, fructose and ethanol.[53,196–200] By contrast, folivores exhibit reduced sensitivity to some bitter compounds, particularly to β-glucopyranosides and glucosinolates.[180,198,201,202] Paradoxically, leaf-eating is also associated with an expansion of other bitter taste receptor genes (*TAS2R*s), allowing folivores to detect a greater breadth of compounds.[177] Folivory has also recently been discovered to lead to relaxed selection on sweet perception.[203] A recent study has also identified adaptive evolution of the umami (or glutamate) taste receptor in primates.[189] The authors found that insectivorous species have a glutamate receptor sensitive to nucleotides that are common in insect prey, while several larger-bodied folivorous species have convergently evolved a receptor sensitive to the glutamate present in leaves to overcome bitter/aversive tastes.

2.6 | Summary of the state of primate sensory ecology

Recent advances in knowledge concerning each of the five senses have been diverse and exciting. Research on primate color vision, especially on the evolution, adaptive potential, and variation in allelic trichromacy among platyrrhines and strepsirrhines has been extensive. This research has provided insights as to the costs and benefits of trichromatic color vision and proposed adaptive explanations for the stable polymorphism of opsin gene alleles. Understanding of olfaction and gustation has been buoyed by identification and characterization of underlying genes, and their variation within and between species. The functional properties of taste receptor genes are also increasingly well characterized. While olfactory receptor genes remain less well understood, important advances in functional genetics may be on the horizon, driven by advances in predictive informatics and cellular assays.

Despite the numerous advances in the past two decades, many lingering gaps in understanding the biology and function of our senses remain and are ripe for future research. Studies of the mechanical senses—hearing and touch—remain rather neglected senses in primate sensory ecology.[54] In the final section, we highlight some of these persistent gaps with the goal of inspiring their study. We also take a step back and reflect on the state of the field and suggest new avenues and approaches that might be fruitful for future sensory ecology research. These avenues are integrative by design, and touch on themes of population variation and adaptation, changes across the lifecourse, interplay of multiple sensory systems, and of the untapped opportunities for studying the environments in which the senses evolve, and their promise for informing our understanding of the animals that inhabit them. We end with an important caveat, a reminder, speaking to the importance of considering nonadaptive explanations when seeking to understand variation and evolution in sensory systems.

3 | EMERGING AND FUTURE RESEARCH

3.1 | Senses that remain poorly understood and ways forward

Touch remains a neglected sense, despite its centrality in hypotheses of primate and human evolution[77,204] and critical roles during food perception. We hope the recent identification of genes underlying discriminative touch and emerging studies of behavior and anatomy will stimulate new interest in exploring primate touch in a more comprehensive way. We present ideas for such a comparative framework in Figure 5. It is also an exciting time to study primate chemosenses, as we are just scratching the surface of comparative olfactory and gustatory biology and dietary ecology. Vanishingly few odors and odor families have been studied in detail, and while researchers have begun to explore sweet, umami and bitter tastes, sour, salty, and fatty tastes remain to be examined in a comparative primate context. Future work will hopefully reveal sources of interspecific variation in odor and taste sensitivities using molecular and/or behavioral psychophysical techniques,[55,74] identifying genotype–phenotype relationships, and uniting these differences with dietary specialization and other aspects of species ecology. While vision remains the best-studied primate sense, studies have tended to focus on color vision, which has been extensively studied across all major primate clades, or visual function in a biomedical context across a limited number of species.[205] Exploring spatial vision and contrast sensitivity functions more comprehensively across taxa, situated in evolutionary contexts, and along with other aspects of the visual system—such as temporal resolution (integration of information over time)—will lead to new discoveries and insights.

Perhaps more importantly, integrative, cross-cutting, and multilevel sensory approaches—especially when studying wild populations—are still in their infancy. We highlight the potential for integrative, multisensory studies to provide insight into processes of sensory integration, and enhancement or dampening of responses from one sensory system on those of another. This approach, advocated in 1972, still resonates today.[206] We also join others[207] in proposing a multilevel approach to studying sensory ecology and evolution by not only studying variation among species, but also among individuals, and over the lifecourse. Another promising, emerging area for advancement in the field of primate sensory ecology is in-depth study of the physical landscapes within which sensory systems must act. Finally, it is always important to pause and question the roles of nonadaptive evolution in shaping sensory system morphology, genetics, and function. Below, we highlight recent studies that have been pushing forward research in these emerging areas, and highlight directions that are particularly promising for future research.

3.2 | Intraspecific variation and local adaptation

Intraspecific variation provides the building blocks for local adaptation, and variation between populations of the same species generates insights into how sensory systems respond to environmental variation.[81,208,209] While visual ecology studies have evaluated the effects of individual color vision phenotype on foraging success,[120,123,132,133] food detection,[210] and measures of reproductive success,[102,135] less effort has been directed toward exploring intraspecific variation in other aspects of primate sensory systems. For most senses, estimates of sensory function (psychophysical, anatomical, or molecular) are collected from one or only a handful of individuals per species, which may obscure the extent of sensory variation present within a population or a species. Indeed, current research suggests dramatic intraspecific variation in some sensory functions. Humans exhibit highly variable functional *OR* gene repertoires,[211,212] with highly individualized patterns of *OR* copy numbers, pseudogenes, and functional variants. Similar intraspecific variation in *OR* genes has been found in dogs[213] and fruit flies[214] and likely also characterizes primates more broadly. This variation influences the number and types of odorants detectable across individuals (humans[215]; fruit flies[214]). Functionally relevant variants in taste receptor genes are also common in populations of humans,[96,177,216] chimpanzees,[217] and in Japanese and Sulawesi macaques (*Macaca fuscata*, *Macaca nigra*).[218,219] In humans, these variants influence individual food preferences and ingestive behavior.[175,181] In the context of primate foraging behavior, intraspecific variation in chemosensory gene repertoires could influence food detection, selection, and chemotaxis and contribute to intraspecific niche partitioning.

If we specifically examine evidence of local adaptation of sensory systems we see evidence of adaptive variation in bitter *TAS2R* genes in chimpanzees[217] and multiple macaque species.[218,219] In Japanese macaques, a "non-taster" variant of the *TAS2R38* gene, well known for its role in detecting bitter substances including limonin found in citrus plants, is at a 29% frequency in the Kii population but completely absent in eight other populations surveyed.[218] Suzuki-Hashido et al. hypothesize that the rapid expansion of the nontaster variant in the Kii population may be the result of local adaptation to exploit the first citrus plants in Japan, which appeared in this region 2800 years ago. Given the heterogeneity of primate habitat types, community assemblages, and plant assemblages between sites, similar instances of local adaptation in sensory systems are likely

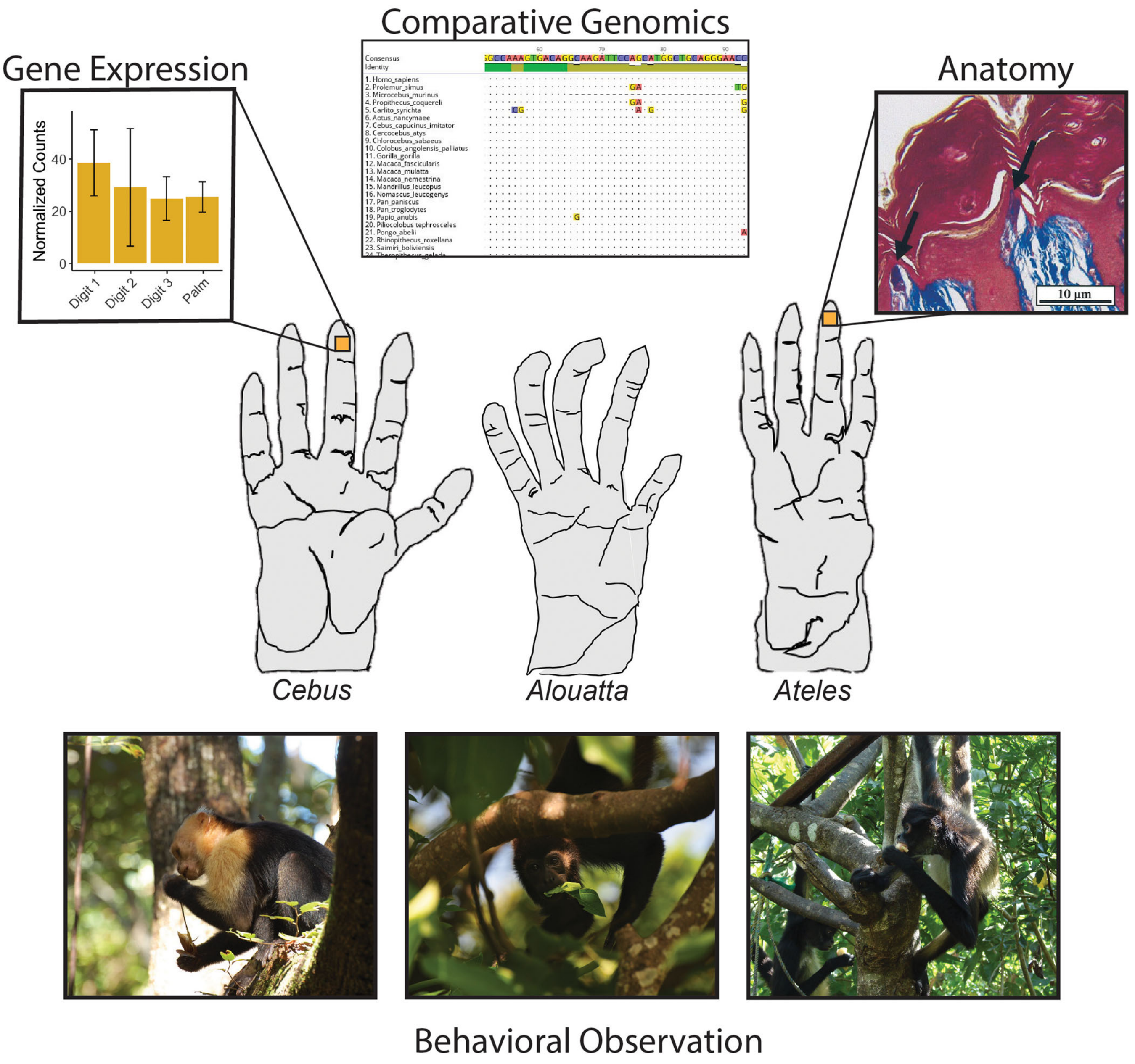


FIGURE 5 Example of a comprehensive approach for sensory ecology. To investigate the sensory ecology of manual touch, a comprehensive approach that unites molecular methods (expression of mechanoreceptor genes in apical pads, comparative genomics of mechanoreceptor genes), anatomical methods (histology of apical pads, hand morphometrics), and behavioral ecology (feeding behaviors, food properties) will be instructive. Gene expression figure is the expression of *Piezo2* in the apical pads of *Macaca* (Velleux, unpublished data). Anatomy image is a histological section of tactile corpuscles (black arrows) in *Piliocolobus* adapted from Hoffmann et al.[162] and reprinted with permission. Hand drawings by C. Veilleux. Photographs: © A. Melin (*Cebus imitator*, left, and *Alouatta paliatta*, middle) and L. Hernández Salazar (*Ateles geoffroyi*, right).

common across primate species, particularly those with more widespread geographic ranges.

3.3 | Sensory ecology across the lifespan

In humans, sensory function changes considerably across the lifespan.[220–222] However, little work has explored the role of age/developmental stage on sensory function or ecology in primates.[223] There are a number of interesting questions situated at the intersection of primate feeding ecology, learning, and sensory system development that suggests this will be a fertile area of research for future primate sensory ecologists in both field and lab settings. For example, how does chemosensation during pregnancy and infancy shape olfactory and taste preferences of infants and juveniles? Previous work in rabbits and humans has demonstrated that tastes and odors experienced by mothers are transmitted to their offspring in utero and via breast milk.[224,225] These chemosensory cues affect the feeding behavior and preferences of their offspring at weaning and can represent a mode of generational sensory learning.[224,226] What role do these mother-based cues play in the development of feeding behavior across primates? Moreover, how does sensory behavior during foraging vary across infancy, adolescence, and adulthood? Melin et al.[123] found that the difference in feeding rates between trichromatic and dichromatic capuchins on conspicuous fruit was more pronounced among juveniles than adult monkeys, possibly suggesting a greater reliance on visual versus nonvisual cues during juvenescence. This highlights the potential for sensory-biased impacts on learning in a foraging context. In general, juveniles experience higher growth-related energetic demands than adults but are less efficient foragers.[227] Questions surrounding the ontogeny of sensory behaviors and impacts of sensory variation in one domain on others during ontogeny have promise to reveal exciting new discoveries (see also Section 3.4).

At the other end of the lifespan, humans exhibit a considerable decline in sensory function with age, with strong impacts of environmental acceleration.[228] Sensory senescence (e.g., age-related declines in sensory function) is common across all senses and affects multiple behavioral domains.[229] In the context of feeding behavior, for example, age-related changes in chemosensation have been linked to changes in human food preferences.[230] Although research has primarily been limited to medical models of human aging, current work suggests that age-related sensory declines also characterize other primates, including mouse lemurs, marmosets, macaques, and chimpanzees.[231–234] It is currently not clear if sensory senescence impacts wild primates. Most studies investigating primate foraging ecology focus on adults, with relatively little focus directed toward consideration of elderly individuals,[235] or age variation among adults as a variable. Do age-related declines in sensory function impact an individual's ability to detect or evaluate foods or move within an arboreal environment? What strategies do older primates employ to mitigate sensory decline? The answers to these questions will provide information on the extent to which sensory senescence is phylogenetically conserved, and contribute to our understanding of healthy aging, and the role of sensory perception and decline across the lifecourse.

3.4 | Multisensory integration

Recent work has highlighted the role of multisensory (or multimodal) integration in the context of primate communication.[236] However, most advances in the study of multisensory foraging arise from the study of insects (e.g., hawkmoths) or model organisms (e.g., mice, zebrafish), where experimenters can block one sense to investigate another.[237–239] Relatively little work has explored multisensory integration during foraging in wild primates, and we know far less about the full nature of their food signals (e.g., VOCs, reflectances, acoustic cues), leaving us disconnected from selective environments. Primates are exploratory foragers, and they often squeeze, sniff, visually inspect, tap, and/or bite fruits before ingesting or rejecting them.[54] Similarly, visual and auditory cues are both important in prey capture,[28] resulting in the "visual orienting reflex" and correlations between visual and auditory acuity in small insectivores.[10]

Although experimental manipulations of wild primates can be challenging (but rewarding, see Siemers et al.[28]), the presence of naturally occurring sensory variation within a single species or closely related species also offers excellent opportunities to investigate sensory interplay. Indeed, the limited data available from these types of comparisons suggest that the sensory modalities employed during food investigation vary across diet items and across foragers.[7,54,73,74] For example, dichromatic capuchin and spider monkeys use their sense of smell more frequently than trichromatic group mates when foraging on fruit, while trichromats use manual touch more frequently than dichromats when foraging specifically on cryptic fruit.[7,60] The standing variation in color vision and other sensory systems seen across Primates opens doors for asking: Does signal structure (fruit size, odor, tastants) and receiver variation (vision, olfactory receptors, taste receptors, hand morphology) impact fruit investigations within and across primate species? Multisensory studies among primates are in their infancy but are well positioned to make foundational contributions toward understanding how food traits shape evolution of animal sensory systems, and how the behaviors of foragers shape the evolution of fruit traits.

3.5 | Sensory landscapes

Physical and biological features of landscapes are inextricably linked to the availability and quality of sensory information, and recent years have seen an explosion of research around the topic of sensory landscapes (Figure 6). For example, the work of Pijanowski et al.[240] propelled rapid growth on the subject of soundscapes, which is defined as all sounds emanating from a given habitat, including sources of geophony (climate and geography), biophony (all wildlife), and anthrophony (human activities). Temporal and spatial variation in the soundscapes of primate habitats is largely unknown, but it is essential if we are to understand the evolution of primate hearing, including derivations within the human lineage.[241] Measuring the audiograms of primates and the acoustic properties of their foods, predators, or vocal signals is critically important but not enough.

Others have extended this concept to other senses, speaking of primate lightscapes and how they affect susceptibility to predation,[113] or aeroscapes, the study of air movement and olfactory-guided foraging (termed anemotaxis). Moving forward, it is tempting to envision discussions of primate odor-scapes and taste-scapes––after all, we know already that fruit sugar content can vary spatially, even within a tree crown.[242] And we anticipate systematic assessments of surface properties (the "touch-scape") encountered by primates; for example, bark and food textures, tools, or the hair of mothers or grooming partners. In all cases, such an approach is expected to shed new light on the sensory specializations that distinguish primates from other mammals.

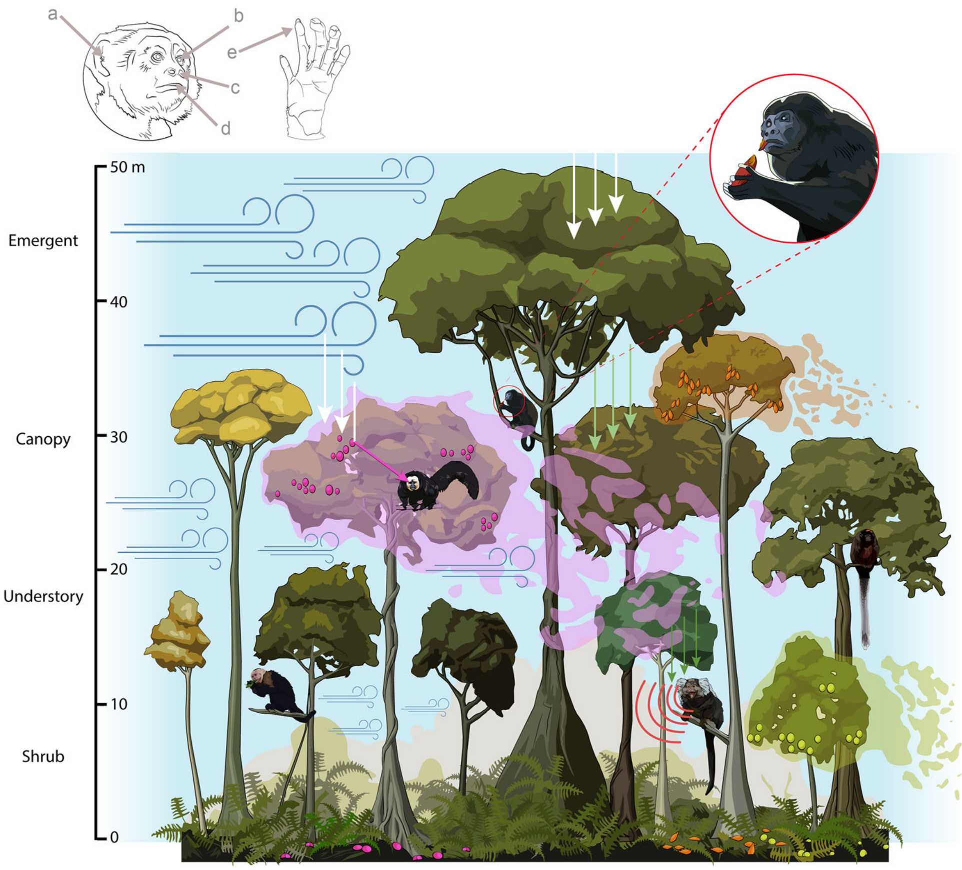


FIGURE 6 Primate senses operate in a complex landscape and aeroscape within which food cues and signals are detected and generate responses, such as travel, evaluation, and consumption behaviors. Environmental variation will influence (a) audition, (b) vision, (c) olfaction, (d) taste, and (e) haptic sensation in ways that might shape foraging strategies. For example, the decreasing size and darkening of the downward-facing vertical arrows (central right) represents the attenuation of wavelengths of light as they travel from the upper canopy to the mid and lower canopy; the change in color from white to light green to saturated green represents the spectral filtering by foliage, as longer (red) and shorter (blue) wavelengths of light are absorbed and middle (green) wavelengths reflected. The light reflected from foods is influenced by the ambient illumination, but also by the visual system and neurological processing of the receiver (pink arrow near saki monkey, center left). Air speeds are anticipated to increase with increasing height in the canopy, as indicated by the size of the blue horizontal wind symbols (moving from left to center), which will impact sound and odor propagation. This can also affect the travel distance of food calls (bottom center), as they propagate through the habitat to act as cues and signals to conspecific and heterospecific foragers. Similarly, increasing turbulence in air flow with canopy height will increasingly disrupt the odor plumes (colorful shading around fruit trees), impacting opportunities and efficiency of food patch detection and anemotaxis. Taste and touch sensation happens over short distances, and are informative during food handling and consumption (capuchin, lower left and howler monkey upper center). Artwork by Brent Adrian.

3.6 | Nonadaptive variation

Over 40 years ago, Gould and Lewontin[243] warned of the dangers of "adaptationist" approaches for understanding biological traits of extant species. At the same time, Kimura[244] promoted the importance of neutral evolution and genetic drift when interpreting genetic variation within species. Despite these concerns, nonadaptive explanations remain relatively underexplored in evolutionary anthropology, including primate sensory ecology. However, there has been a recent shift to explicitly considering nonadaptive evolutionary mechanisms, including in morphometrics[245] and primate behavioral biology.[246] Primate sensory ecology has followed suit. Nonadaptive mechanisms (e.g., drift) have clearly influenced sensory anatomy, sensory genes, and sensory function. For example, primates, like all mammals, exhibit more globular eye shapes relative to other vertebrates due to a nocturnal bottleneck in early mammal evolution.[247] Variation of that globular design can be influenced by ecological (e.g., activity pattern,[248] habitat preference[249]), physiological, or genetic factors. Other sensory features may represent exaptations[243] from a previous evolutionary context. Routine trichromacy, for example, is hypothesized to have evolved within a feeding context,[122,127] but may have been exapted in catarrhines to detect social signals.[250] Similarly, while *OR* genes are likely associated with diet,[37] they have also been linked to variation in the major histocompatibility complex system, which is involved in both immune response and mate choice.[251–253] Variation in sensory genes can also result from linkage disequilibrium (wherein a selective sweep may be acting on a neighboring nonsensory locus) or mechanisms of genetic drift, e.g., population bottlenecks. As a recent example, Jacobs et al.[104,254] investigated competing explanations for the presence of uniform LWS dichromatic color vision in red-bellied lemurs (*Eulemur rubriventer*) at Ranomafana National Park in Madagascar. They found equivocal evidence in support of a population bottleneck, suggesting that the *MWS* allele may have been lost due to drift,[254] although they also did not rule out adaptive mechanisms.[104]

Primate sensory ecologists investigating potential adaptations should work to situate sensory features within a comparative phylogenetic context, and if possible, explicitly test both adaptive and nonadaptive mechanisms. Moreover, we need more work explicitly linking sensory behavior or function to putatively adaptive anatomy and genes (e.g., genetic variants or gene repertoire). While many studies have identified interspecific variation in aspects of sensory anatomy (e.g., brain region size,[67] binocular field overlap[78]) or sensory genes (e.g., olfactory gene repertoire size[37]), we have little understanding of how this variation influences the way primates use their senses in the natural world. We need more field studies and captive experiments of sensory behavior during ecologically relevant tasks (e.g., feeding, locomotion). Standardized methods of quantifying sensory behavior would greatly enhance this effort (e.g., see a recent ethogram for sensory behaviors[6]).

4 | CONCLUSIONS

Primate sensory ecology emerged in the 1970s from the work of comparative anatomists and physiologists, and a few field researchers, notably Georges Pariente and D. Max Snodderly. This research was essential to understanding the underlying variability of primate sensory systems and inferring functional ecological relationships. By the 1990s, a new wave of field studies, led by geneticists and experimental psychologists, began to focus on the sensory (visual) attributes of natural food objects. It was this work, reviewed by Dominy et al. in 2001, that wrote the blueprint for many primatologists, who, in turn, began to kick the tires of treasured assumptions. Primatologists of the 2000s and 2010s focused their efforts on integrating systematic behavioral observations with a multitude of additional analytical tools, from genotyping individual animals to myriad measures of food physico-chemical properties. Other researchers adopted experimental approaches, using carefully selected and controlled stimuli in captive, semicaptive, and field settings. Importantly, as the subject grew and diversified, cross-cutting conversations and collaborations emerged that changed the direction, scope, and scale of primate sensory ecology. Buoyed by technical advances (portable instrumentation, genetic sequencing, etc.) and the increasing durée of long-term field sites, many primatologists began to produce, rather than test ex post facto, important theoretical advances.

For example, the "poor" (microsmatic) olfactory abilities of primates was a matter of conventional wisdom during the 1990s.[255] Yet, behavioral studies have demonstrated that primates are highly sensitive to some odors, and the use of sniffing behaviors is widespread. How then to interpret the simplification of the olfactory genes and anatomy of some lineages? The answer likely lies in taking a more nuanced approach that asks which odors are relevant and under what environmental conditions is olfaction engaged. Here, we discuss foraging but integrative approaches that consider social and other fitness-related challenges are certainly needed for a holistic understanding. As another example, the polymorphic color vision of many primates was often described as a suboptimal "stage" on the path to uniform trichromatic vision during the late 1980s and early 2000s,[256,257] a phrasing that risks teleological interpretation. Today, the emerging picture is one in which allelic variation is widespread and maintained under balancing selection, with differential foraging advantages associated with each color vision phenotype.[102,123]

We are still in the early days of understanding our sensory world with impactful discoveries on the horizon. Primate sensory ecology makes important contributions to understanding the variation, adaptation, and evolution of our species and lineage. It sits at the intersection of behavior, ecology, anatomy, and genetics, and in doing so, serves as a bridge between the ecology and behavior of extant primates and paleoecological reconstructions of fossil taxa. Identifying how diet and ecology shapes primate sensory systems informs hypotheses of primate origins and adaptive radiation, our understanding of extant variation, and is essential for planning conservation efforts.[113] Looking to the future, we join and amplify the voices of others in biological anthropology,[206,245] and sensory biology more generally,[207] who have been proponents of incorporating landscape-level approaches and increasing multisensory, longitudinal, and cross-cutting approaches to studying the sensory ecology and evolution of primates. We hope the new directions we propose will spur innovative new research during the decades to come.

ACKNOWLEDGMENTS

During the writing of this manuscript, ADM was funded by the Canada Research Chairs program (950-231257) and a National Science and Engineering Research Council (NSERC) Discovery Grant (RGPIN-2017-03782) and Accelerator Supplement.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Carrie C. Veilleux https://orcid.org/0000-0003-4441-7521
Nathaniel J. Dominy http://orcid.org/0000-0001-5916-418X
Amanda D. Melin http://orcid.org/0000-0002-0612-2514

REFERENCES

1. Pessoa DMA et al. 2014. The adaptive value of primate color vision for predator detection. Am J Primatol 76:721–729.
2. Miller LE, editor. 2002. *Eat or be eaten: predator sensitive foraging among primates*. Cambridge: Cambridge University Press.

3. Ghazanfar AA, Santos LR. 2004. Primate brains in the wild: the sensory bases for social interactions. Nat Rev Neurosci 5:603–616.
4. Petersen RM, Higham JP. 2020. The role of sexual selection in the evolution of facial displays in male non-human primates and men. Adapt Hum Behav Physiol 6:249–276.
5. Dominy NJ et al. 2001. The sensory ecology of primate food perception. Evol Anthropol 10:171–186.
6. Melin AD et al. 2018. Data collection in field primatology: a renewed look at measuring foraging behaviour. In: Kalbitzer U, Jack KM, editors. *Primate Life Hist Sex Roles Adapt—Essays Honour Linda M Fedigan*. New York, NY: Springer. p 161–192.
7. Melin AD et al. 2022. Anatomy and dietary specialization influence sensory behaviour among sympatric primates. Proc R Soc B Biol Sci 289:20220847.
8. Huang F-Y et al. 2021. Preferences for nutrients and sensory food qualities identify biological sources of economic values in monkeys. Proc Natl Acad Sci USA 118:e2101954118.
9. Coleman MN, Ross CF. 2004. Primate auditory diversity and its influence on hearing performance. Anat Rec A Discov Mol Cell Evol Biol 281A:1123–1137.
10. Heffner RS. 2004. Primate hearing from a mammalian perspective. Anat Rec A Discov Mol Cell Evol Biol 281A:1111–1122.
11. Hackley SA. 2015. Evidence for a vestigial pinna-orienting system in humans. Psychophysiology 52:1263–1270.
12. Kirk EC, Gosselin-Ildari AD. 2009. Cochlear labyrinth volume and hearing abilities in primates. Anat Rec 292:765–776.
13. Stangor C, Walinga J. 2014. Introduction to Psychology—1st Canadian edition. Victoria, B.C.: Bccampus. Retrieved from https://opentextbc.ca/introductionto
14. Coleman MN, Colbert MW. 2010. Correlations between auditory structures and hearing sensitivity in non-human primates. J Morphol 271:511–532.
15. Ramsier MA, Rauschecker JP. 2017. Primate audition: reception, perception, and ecology. In: Quam RM et al., editors. *Primate Hear Commun*. Cham: Springer International Publishing. p 47–77.
16. Coleman MN. 2009. What do primates hear? A meta-analysis of all known nonhuman primate behavioral audiograms. Int J Primatol 30:55–91.
17. Ramsier MA et al. 2012. Primate communication in the pure ultrasound. Biol Lett Royal Society 8:508–511.
18. Ramsier MA et al. 2012. Social drive and the evolution of primate hearing. Philos Trans R Soc B Biol Sci Royal Society 367: 1860–1868.
19. Ramsier MA et al. 2019. Audiograms of howling monkeys: are extreme loud calls the result of runaway selection? bioRxiv 539023. https://doi.org/10.1101/539023
20. Frenzel H et al. 2012. A genetic basis for mechanosensory traits in humans. PLoS Biol 10:e1001318.
21. Bankoff RJ et al. 2017. Testing convergent evolution in auditory processing genes between echolocating mammals and the aye-aye, a percussive-foraging primate. Genome Biol Evol 9:1978–1989.
22. Erickson CJ et al. 1998. percussive foraging: stimuli for prey location by aye-ayes (*Daubentonia madagascariensis*). Int J Primatol 19:111–122.
23. Waser PM, Brown CH. 1986. Habitat acoustics and primate communication. Am J Primatol 10:135–154.
24. Oliveira DAG, Ades C. 2004. Long-distance calls in Neotropical primates. An Acad Bras Ciênc Academia Brasileira de Ciências 76: 393–398.
25. Fedurek P et al. 2014. Social and ecological correlates of long-distance pant hoot calls in male chimpanzees. Behav Ecol Sociobiol 68:1345–1355.
26. Notman H, Rendall D. 2005. Contextual variation in chimpanzee pant hoots and its implications for referential communication. Anim Behav 70:177–190.
27. Sugiyama J et al. 1994. Firmness measurement of muskmelons by acoustic impulse transmission. Trans ASAE 37:1235–1241.
28. Siemers BM et al. 2007. Sensory basis of food detection in wild *Microcebus murinus*. Int J Primatol 28:291.
29. Brumm H et al. 2004. Acoustic communication in noise: regulation of call characteristics in a New World monkey. J Exp Biol 207: 443–448.
30. Goerlitz HR. 2018. Weather conditions determine attenuation and speed of sound: environmental limitations for monitoring and analyzing bat echolocation. Ecol Evol 8:5090–5100.
31. Geerah DR et al. 2019. The use of ultrasonic communication to maintain social cohesion in the Javan slow loris (*Nycticebus javanicus*). Folia Primatol (Basel) 90:392–403.
32. Garrett EC, Steiper ME. 2014. Strong links between genomic and anatomical diversity in both mammalian olfactory chemosensory systems. Proc R Soc B Biol Sci 281:20132828.
33. Nevo O, Heymann EW. 2015. Led by the nose: olfaction in primate feeding ecology. Evol Anthropol 24:137–148.
34. Smith TD et al. 2011. The vomeronasal organ of new world monkeys (Platyrrhini). Anat Rec 294:2158–2178.
35. Bhatnagar KP, Meisami E. 1998. Vomeronasal organ in bats and primates: extremes of structural variability and its phylogenetic implications. Microsc Res Tech 43:465–475.
36. Heymann EW. 2006. The neglected sense-olfaction in primate behavior, ecology, and evolution. Am J Primatol 68:519–524.
37. Niimura Y et al. 2018. Acceleration of olfactory receptor gene loss in primate evolution: possible link to anatomical change in sensory systems and dietary transition. Mol Biol Evol 35:1437–1450.
38. Heritage S. 2014. Modeling olfactory bulb evolution through primate phylogeny. PLoS One 9:e113904.
39. Smith TD et al. 2004. Distribution of olfactory epithelium in the primate nasal cavity: are microsmia and macrosmia valid morphological concepts? Anat Rec A Discov Mol Cell Evol Biol 281: 1173–1181.
40. Kawamura S, Melin AD. 2017. Evolution of genes for color vision and the chemical senses in primates. In: Saitou N, editor. *Evol Hum Genome Genes*. Tokyo: Springer Japan. p 181–216.
41. Bushdid C et al. 2014. Humans can discriminate more than 1 trillion olfactory stimuli. Science 343:1370–1372.
42. Adipietro KA et al. 2012. Functional evolution of mammalian odorant receptors. PLoS Genet 8:e1002821.
43. Niimura Y et al. 2014. Extreme expansion of the olfactory receptor gene repertoire in African elephants and evolutionary dynamics of orthologous gene groups in 13 placental mammals. Genome Res 24:1485–1496.
44. Hoover KC et al. 2015. Global survey of variation in a human olfactory receptor gene reveals signatures of non-neutral evolution. Chem Senses 40:481–488.
45. Hayden S et al. 2010. Ecological adaptation determines functional mammalian olfactory subgenomes. Genome Res 20:1–9.
46. Hoover KC. 2010. Smell with inspiration: the evolutionary significance of olfaction. Am J Phys Anthropol 143(suppl 51): 63–74.
47. Heymann EW. 2011. Florivory, nectarivory, and pollination—a review of primate-flower interactions. Ecotropica 17:41–52.
48. Valenta K et al. 2013. Colour and odour drive fruit selection and seed dispersal by mouse lemurs. Sci Rep 3:2424.
49. Nevo O et al. 2016. Fruit odor as a ripeness signal for seed-dispersing primates? A case study on four neotropical plant species. J Chem Ecol 42:323–328.

50. Simin T et al. 2021. Volatile organic compound emission in tundra shrubs—dependence on species characteristics and the near-surface environment. Environ Exp Bot 184:104387.
51. Thompson CL et al. 2020. What smells? Developing in-field methods to characterize the chemical composition of wild mammalian scent cues. Ecol Evol 10:4691–4701.
52. Thompson CL et al. 2018. Do common marmosets (*Callithrix jacchus*) use scent to communicate information about food resources? Folia Primatol (Basel) 89:305–315.
53. Dominy NJ. 2004. Fruits, fingers, and fermentation: the sensory cues available to foraging primates. Integr Comp Biol 44:295–303.
54. Dominy NJ et al. 2016. How chimpanzees integrate sensory information to select figs. Interface Focus 6:20160001.
55. Laska M, Seibt A. 2002. Olfactory sensitivity for aliphatic esters in squirrel monkeys and pigtail macaques. Behav Brain Res 134: 165–174.
56. Porter J et al. 2007. Mechanisms of scent-tracking in humans. Nat Neurosci 10:nn1819.
57. Cunningham EP et al. 2021. Ring-tailed lemurs (*Lemur catta*) use olfaction to locate distant fruit. Am J Phys Anthropol 175: 300–307.
58. Melin AD et al. 2009. Fig foraging by dichromatic and trichromatic *Cebus capucinus* in a tropical dry forest. Int J Primatol 30:753.
59. Pablo-Rodríguez M et al. 2015. The role of sucrose and sensory systems in fruit selection and consumption of *Ateles geoffroyi* in Yucatan, Mexico. J Trop Ecol 31:213–219.
60. Melin AD et al. 2019. Fruit scent and observer colour vision shape food-selection strategies in wild capuchin monkeys. Nat Commun 10:1–9.
61. Lomáscolo SB, Schaefer HM. 2010. Signal convergence in fruits: a result of selection by frugivores? J Evol Biol 23:614–624.
62. Nevo O et al. 2018. Frugivores and the evolution of fruit colour. Biol Lett 14:20180377.
63. Nevo O et al. 2018. Fruit scent as an evolved signal to primate seed dispersal. Sci Adv 4:eaat4871
64. Petrova M et al. 2008. Evaluation of trigeminal sensitivity to ammonia in asthmatics and healthy human volunteers. Inhal Toxicol 20:1085–1092.
65. Reiffenstein RJ et al. 1992. Toxicology of hydrogen sulfide. Annu Rev Pharmacol Toxicol 32:109–134.
66. Case TI et al. 2020. The animal origins of disgust: reports of basic disgust in nonhuman great apes. Evol Behav Sci 14:231–260.
67. DeCasien AR, Higham JP. 2019. Primate mosaic brain evolution reflects selection on sensory and cognitive specialization. Nat Ecol Evol 3:1483–1493.
68. Müller-Schwarze D. 2006. *Chemical ecology of vertebrates*. New York: Cambridge University Press.
69. Conchou L et al. 2019. Insect odorscapes: from plant volatiles to natural olfactory scenes. Front Physiol 10:972.
70. DePasquale A et al. 2022. Aeroscapes and the sensory ecology of olfaction in a tropical dry forest. Front Ecol Evol 10:849281.
71. Bolen RH, Green SM. 1997. Use of olfactory cues in foraging by owl monkeys (Aotus nancymai) and capuchin monkeys (Cebus apella). J Comp Psychol Wash DC 1983 111:152–158.
72. Bicca-Marques JC, Garber PA. 2004. Use of spatial, visual, and olfactory information during foraging in wild nocturnal and diurnal anthropoids: a field experiment comparing Aotus, Callicebus, and Saguinus. Am J Primatol 62:171–187.
73. Laska M et al. 2007. Which senses play a role in nonhuman primate food selection? A comparison between squirrel monkeys and spider monkeys. Am J Primatol 69:282–294.
74. Nevo O et al. 2015. Chemical recognition of fruit ripeness in spider monkeys (*Ateles geoffroyi*). Sci Rep 5:14895.
75. Rushmore J et al. 2012. Sight or scent: lemur sensory reliance in detecting food quality varies with feeding ecology. PloS One 7:e41558.
76. Hughes GM et al. 2014. Loss of olfactory receptor function in hominin evolution. PloS One 9:e84714.
77. Cartmill M. 1992. New views on primate origins. Evol Anthropol Issues News Rev 1:105–111.
78. Heesy CP. 2008. Ecomorphology of orbit orientation and the adaptive significance of binocular vision in primates and other mammals. Brain Behav Evol 71:54–67.
79. Veilleux CC, Kirk EC. 2014. Visual acuity in mammals: effects of eye size and ecology. Brain Behav Evol 83:43–53.
80. Melin AD et al. 2013. Inferred L/M cone opsin polymorphism of ancestral tarsiers sheds dim light on the origin of anthropoid primates. Proc Biol Sci 280:20130189.
81. Veilleux CC et al. 2013. Nocturnal light environments influence color vision and signatures of selection on the *OPN1SW* opsin gene in nocturnal lemurs. Mol Biol Evol 30:1420–1437.
82. Jacobs RL et al. 2017. Novel opsin gene variation in large-bodied, diurnal lemurs. Biol Lett 13:20170050.
83. Caves EM, Johnsen S. 2018. AcuityView: an R package for portraying the effects of visual acuity on scenes observed by an animal. Methods Ecol Evol 9:793–797.
84. Eibenstein A et al. 2005. Modern psychophysical tests to assess olfactory function. Neurol Sci 26:147–155.
85. Wolfe JM et al. 2009. *Sensation & perception*. 2nd ed. Sunderland, MA: Sinauer Associates.
86. Seubert J et al. 2013. Orbitofrontal cortex and olfactory bulb volume predict distinct aspects of olfactory performance in healthy subjects. Cereb Cortex 23:2448–2456.
87. Veilleux CC. 2020. Seeing in the dark: visual function and ecology of lorises and pottos. In: Nekaris KAI, Burrows AM, editors. *Evol Ecology Conserv Lorises Pottos*. Cambridge, UK: Cambridge University Press. p 174–186.
88. Kirk EC, Kay RF. 2004. The evolution of high visual acuity in the Anthropoidea. In: Ross CF, Kay RF, editors. *Anthr Orig New Vis*. New York: Kluwer Academic/Plenum Publishers. p 539–602.
89. Jacobs GH. 2009. Evolution of colour vision in mammals. Philos Trans R Soc B Biol Sci 364:2957–2967.
90. Moreira LAA et al. 2019. Platyrrhine color signals: new horizons to pursue. Evol Anthropol Issues News Rev 28:236–248.
91. Jacobs GH, Williams GA. 2001. The prevalence of defective color vision in Old World monkeys and apes. Color Res Appl 26: S123–S127.
92. Verrelli BC et al. 2008. Different selective pressures shape the molecular evolution of color vision in chimpanzee and human populations. Mol Biol Evol 25:2735–2743.
93. Hiwatashi T et al. 2011. Gene conversion and purifying selection shape nucleotide variation in gibbon L/M opsin genes. BMC Evol Biol 11:312.
94. Munds R et al. Is primate cone ratio variation functional and adaptive (in review). Proc Royal Soc B.
95. Munds R et al. 2022. Variation and heritability of retinal cone ratios in a free-ranging population of rhesus macaques. Evolution 76: 1776—1789.
96. Veilleux CC. 2019. Sensory polymorphisms and dietary adaptation. In: O'Rourke DH, editor. *Companion Anthropol Genet*. New York: John Wiley & Sons, Ltd. p 233–250.
97. Veilleux CC et al. 2021. Color vision and niche partitioning in a diverse neotropical primate community in lowland Amazonian Ecuador. Ecol Evol 11:5742–5758.
98. Corso J et al. 2016. Highly polymorphic colour vision in a New World monkey with red facial skin, the bald uakari (*Cacajao calvus*). Proc R Soc B 283:20160067.
99. Goulart VDLR et al. 2017. Medium/Long wavelength sensitive opsin diversity in Pitheciidae. Sci Rep 7:7737.
100. Kawamura S, Kubotera N. 2004. Ancestral loss of short wave-sensitive cone visual pigment in lorisiform prosimians, contrasting

with its strict conservation in other prosimians. J Mol Evol 58: 314–321.

101. Veilleux CC, Bolnick DA. 2009. Opsin gene polymorphism predicts trichromacy in a cathemeral lemur. Am J Primatol 71:86–90.
102. Veilleux CC et al. 2016. Group benefit associated with polymorphic trichromacy in a Malagasy primate (*Propithecus verreauxi*). Sci Rep 6:srep38418
103. Valenta K et al. 2015. Sensory integration during foraging: the importance of fruit hardness, colour, and odour to brown lemurs. Behav Ecol Sociobiol 69:1855–1865.
104. Jacobs RL et al. 2019. Less is more: lemurs (*Eulemur* spp.) may benefit from loss of trichromatic vision. Behav Ecol Sociobiol 77:22.
105. Caves EM et al. 2018. Visual acuity and the evolution of signals. Trends Ecol Evol 33:358–372.
106. Stevens M et al. 2009. Studying primate color: towards visual system-dependent methods. Int J Primatol 30:893–917.
107. Higham JP et al. 2010. Color signal information content and the eye of the beholder: a case study in the rhesus macaque. Behav Ecol 21:739–746.
108. Troscianko J, Stevens M. 2015. Image calibration and analysis toolbox—a free software suite for objectively measuring reflectance, colour and pattern. Methods Ecol Evol 6:1320–1331.
109. Osorio D et al. 2004. Detection of fruit and the selection of primate visual pigments for color vision. Am Nat 164:696–708.
110. Endler JA. 1993. The color of light in forests and its implications. Ecol Monogr 63:2–27.
111. Anhuf D, Rollenbeck R. 2001. Canopy structure of the Rio Surumoni rain forest (Venezuela) and its influence on microclimate. Ecotropica 7:21–32.
112. Veilleux CC, Cummings ME. 2012. Nocturnal light environments and species ecology: implications for nocturnal color vision in forests. J Exp Biol 215:4085–4096.
113. Dominy NJ, Melin AD. 2020. Liminal light and primate evolution. Annu Rev Anthropol 49:257–276.
114. Melin AD et al. 2012. Why aye-ayes see blue. Am J Primatol 74: 185–192.
115. Veilleux CC et al. 2014. Opsin genes and visual ecology in a nocturnal folivorous lemur. Int J Primatol 35:88–107.
116. Moritz GL et al. 2017. Functional preservation and variation in the cone opsin genes of nocturnal tarsiers. Phil Trans R Soc B 372:20160075.
117. Changizi MA, Shimojo S. 2008. "X-ray vision" and the evolution of forward-facing eyes. J Theor Biol 254:756–767.
118. Melin AD et al. 2010. Can color vision variation explain sex differences in invertebrate foraging by capuchin monkeys? Curent Zool 56:300–312.
119. Caine NG et al. 2010. A foraging advantage for dichromatic marmosets (*Callithrix geoffroyi*) at low light intensity. Biol Lett 6: 36–38.
120. Smith AC et al. 2012. Effect of colour vision status on insect prey capture efficiency of captive and wild tamarins (*Saguinus* spp.). Anim Behav 83:479–486.
121. Bunce JA et al. 2011. Color vision variation and foraging behavior in wild neotropical titi monkeys (*Callicebus brunneus*): possible mediating roles for spatial memory and reproductive status. Int J Primatol 32:1058–1075.
122. Melin AD et al. 2017. Howler monkey foraging ecology suggests convergent evolution of routine trichromacy as an adaptation for folivory. Ecol Evol 7:1421–1434.
123. Melin AD et al. 2017. Trichromacy increases fruit intake rates of wild capuchins (*Cebus capucinus imitator*). Proc Natl Acad Sci 114: 10402–10407.
124. Dominy NJ, Lucas PW. 2004. Significance of color, calories, and climate to the visual ecology of catarrhines. Am J Primatol 62: 189–207.
125. Riba-Hernández P et al. 2005. Sugar concentration of fruits and their detection via color in the Central American spider monkey (*Ateles geoffroyi*). Am J Primatol 67:411–423.
126. Valenta K et al. 2016. Fruit ripening signals and cues in a Madagascan dry forest: haptic indicators reliably indicate fruit ripeness to dichromatic lemurs. Evol Biol 43:344–355.
127. Dominy NJ et al. 2003. Historical contingency in the evolution of primate color vision. J Hum Evol 44:25–45.
128. Hawes JE, Peres CA. 2014. Ecological correlates of trophic status and frugivory in neotropical primates. Oikos 123:365–377.
129. Hiwatashi T et al. 2010. An explicit signature of balancing selection for color-vision variation in new world monkeys. Mol Biol Evol 27: 453–464.
130. Saito A et al. 2005. Advantage of dichromats over trichromats in discrimination of color-camouflaged stimuli in nonhuman primates. Am J Primatol 67:425–436.
131. Troscianko J et al. 2017. Relative advantages of dichromatic and trichromatic color vision in camouflage breaking. Behav Ecol 28: 556–564.
132. Vogel ER et al. 2007. Effect of color vision phenotype on the foraging of wild white-faced capuchins, *Cebus capucinus*. Behav Ecol 18:292–297.
133. Hiramatsu C et al. 2008. Importance of achromatic contrast in short-range fruit foraging of primates. PLoS One 3:e3356.
134. Hogan JD et al. 2018. Trichromatic perception of flower colour improves resource detection among New World monkeys. Sci Rep 8:10883.
135. Fedigan LM et al. 2014. The heterozygote superiority hypothesis for polymorphic color vision is not supported by long-term fitness data from wild neotropical monkeys. PloS One 9:e84872.
136. DePasquale AD et al. 2021. Testing the niche differentiation hypothesis in wild capuchin monkeys with polymorphic color vision. Behav Ecol 32:599–608.
137. Bearder SK et al. 2006. A re-evaluation of the role of vision in the activity and communication of nocturnal primates. Folia Primatol (Basel) 77:50–71.
138. Coimbra JP et al. 2016. The topographic organization of retinal ganglion cell density and spatial resolving power in an unusual arboreal and slow-moving strepsirhine primate, the potto (*Perodicticus potto*). Brain Behav Evol 87:4–18.
139. Gursky S. 2003. Lunar philia in a nocturnal primate. Int J Primatol 24:351–367.
140. Veilleux CC, Heesy CP.Visual system of the only nocturnal anthropoid, *Aotus*—the owl monkey. In: Fernandez-Duque E, editor. *Owl Monkeys—Biol Adapt Radiat Behav Ecol Noct Primate Am*. In press. New York: Springer. https://link.springer.com/book/9783031135545
141. Fernández-Duque E et al. 2010. Moonstruck primates: owl monkeys (Aotus) need moonlight for nocturnal activity in their natural environment. PLoS One 5:e12572.
142. Nekaris KAI. 2005. Foraging behaviour of the slender loris (*Loris lydekkerianus lydekkerianus*): implications for theories of primate origins. J Hum Evol 49:289–300.
143. Perry GH et al. 2007. Signatures of functional constraint at aye-aye opsin genes: the potential of adaptive color vision in a nocturnal primate. Mol Biol Evol 24:1963–1970.
144. Moritz GL, Dominy NJ. 2010. Selective advantages of mono- and dichromatic vision among nocturnal primates. J Vis 10:1.
145. Moritz GL. 2015. *Primate origins through the lens of functional and degenerate cone opsins [Ph.D. Dissertation]*. Dartmouth College.
146. Gaston KJ. 2019. nighttime ecology: the "nocturnal problem" revisited. Am Nat 193:481–502.
147. Freitag FB, Pessoa DMA. 2012. Effect of luminosity on color discrimination of dichromatic marmosets (*Callithrix jacchus*). JOSA A 29:A216–A222.

148. Zimmerman A et al. 2014. The gentle touch receptors of mammalian skin. Science 346:950–954.
149. Saal HP, Bensmaia SJ. 2014. Touch is a team effort: interplay of submodalities in cutaneous sensibility. Trends Neurosci 37: 689–697.
150. Organ JM et al. 2011. Mechanoreceptivity of prehensile tail skin varies between ateline and cebine primates. Anat Rec 294:2064–2072.
151. Johansson RS, Vallbo AB. 1979. Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptive units in glabrous skin. J Physiol 286:283–300.
152. Hennig EM, Sterzing T. 2009. Sensitivity mapping of the human foot: thresholds at 30 skin locations. Foot Ankle 30:986–991.
153. Mancini F et al. 2014. Whole-body mapping of spatial acuity for pain and touch. Ann Neurol 75:917–924.
154. Poole K et al. 2014. Tuning Piezo ion channels to detect molecular-scale movements relevant for fine touch. Nat Commun 5:3520.
155. Walsh CM et al. 2015. Mammalian touch catches up. Curr Opin Neurobiol 34:133–139.
156. Schneider ER et al. 2019. A cross-species analysis reveals a general role for Piezo2 in mechanosensory specialization of trigeminal ganglia from tactile specialist birds. Cell Rep 26:1979–1987.e3.
157. Schwaller F et al. 2021. USH2A is a Meissner's corpuscle protein necessary for normal vibration sensing in mice and humans. Nat Neurosci Nature Publishing Group 24:74–81.
158. Sánchez-Solano KG et al. 2022. Non-visual senses in fruit selection by the mantled howler monkey (*Alouatta palliata*). Primates 63: 293–303.
159. Laska M. 1998. Laterality in the use of the prehensile tail in the spider monkey (*Ateles geoffroyi*). Cortex 34:123–130.
160. Nelson EL, Kendall GA. 2018. Goal-directed tail use in Colombian spider monkeys (*Ateles fusciceps rufiventris*) is highly lateralized. J Comp Psychol 132:40–47.
161. Williamson RE et al. 2021. Sharing spaces: niche differentiation in diet and substrate use among wild capuchin monkeys. Anim Behav 179:317–338.
162. Hoffmann JN et al. 2004. Meissner corpuscles and somatosensory acuity: The prehensile appendages of primates and elephants. Anat Rec 281A:1138–1147.
163. Muchlinski MN et al. 2010. Evidence for dietary niche separation based on infraorbital foramen size variation among subfossil lemurs. Folia Primatol (Basel) 81:330–345.
164. Fragaszy DM et al. 2013. Wild bearded capuchin monkeys (*Sapajus libidinosus*) strategically place nuts in a stable position during nut-cracking. PLoS One 8:e56182.
165. Melin AD et al. 2014. Seasonality, extractive foraging and the evolution of primate sensorimotor intelligence. J Hum Evol 71: 77–86.
166. Trulsson M. 2006. Sensory-motor function of human periodontal mechanoreceptors. J Oral Rehabil 33:262–273.
167. Levy JH, Dong WK. 2022. Vibration perception thresholds of human vital and nonvital maxillary incisors. Arch Oral Biol 139:105426.
168. Miles BL et al. 2018. Comparative tactile sensitivity of the fingertip and apical tongue using complex and pure tactile tasks. Physiol Behav 194:515–521.
169. Muchlinski MN. 2010. Ecological correlates of infraorbital foramen area in primates. Am J Phys Anthropol 141:131–141.
170. Muchlinski MN. 2010. A comparative analysis of vibrissa count and infraorbital foramen area in primates and other mammals. J Hum Evol 58:447–473.
171. Muchlinski MN, Kirk EC. 2017. A comparative analysis of infraorbital foramen size in Paleogene euarchontans. J Hum Evol 105:57–68.
172. Verendeev A et al. 2015. Comparative analysis of Meissner's corpuscles in the fingertips of primates. J Anat 227:72–80.
173. Meyerhof W. 2005. Elucidation of mammalian bitter taste. Rev Physiol Biochem Pharmacol 154:37–72.
174. Running CA et al. 2015. Oleogustus: the unique taste of fat. Chem Senses 40:507–516.
175. Chamoun E et al. 2018. A review of the associations between single nucleotide polymorphisms in taste receptors, eating behaviors, and health. Crit Rev Food Sci Nutr 58:194–207.
176. Chandrashekar J et al. 2006. The receptors and cells for mammalian taste. Nature 444:288–294.
177. Hayakawa T et al. 2014. Frequent expansions of the bitter taste receptor gene repertoire during evolution of mammals in the Euarchontoglires clade. Mol Biol Evol 31:2018–2031.
178. Antinucci M, Risso D. 2017. A matter of taste: lineage-specific loss of function of taste receptor genes in vertebrates. Front Mol Biosci 4:81.
179. Lalueza-Fox C et al. 2009. Bitter taste perception in Neanderthals through the analysis of the *TAS2R38* gene. Biol Lett 5:809–811.
180. Imai H et al. 2012. Functional diversity of bitter taste receptor TAS2R16 in primates. Biol Lett 8:652–656.
181. Hayes JE et al. 2013. Do polymorphisms in chemosensory genes matter for human ingestive behavior? Food Qual Prefer 30:202–216.
182. Campbell MC et al. 2014. Origin and differential selection of allelic variation at *TAS2R16* associated with salicin bitter taste sensitivity in Africa. Mol Biol Evol 31:288–302.
183. Dias AG et al. 2013. Genetic variation in putative salt taste receptors and salt taste perception in humans. Chem Senses 38:137–145.
184. Ishimaru Y. 2015. Molecular mechanisms underlying the reception and transmission of sour taste information. Biosci Biotechnol Biochem 79:171–176.
185. Hladik CM, Simmen B. 1996. Taste perception and feeding behavior in non-human primates and human populations. Evol Anthropol 5:58–71.
186. Simmen B, Hladik CM. 1998. Sweet and bitter taste discrimination in primates: scaling effects across species. Folia Primatol (Basel) 69: 129–138.
187. Laska M. 1996. Taste preference thresholds for food-associated sugars in the squirrel monkey (*Saimiri sciureus*). Primates 37:91–95.
188. Pereira S et al. 2021. Taste responsiveness of chimpanzees (*Pan troglodytes*) and black-handed spider monkeys (*Ateles geoffroyi)* to eight substances tasting sweet to humans. Physiol Behav 238:113470.
189. Toda Y et al. 2021. Evolution of the primate glutamate taste sensor from a nucleotide sensor. Curr Biol 31:4641–4649.e5.
190. Laska M et al. 2009. Gustatory responsiveness to six bitter tastants in three species of nonhuman primates. J Chem Ecol 35:560–571.
191. Nishi E et al. 2016. High maltose sensitivity of sweet taste receptors in the Japanese macaque (*Macaca fuscata*). Sci Rep 6:39352.
192. Nicklasson S et al. 2018. Taste responsiveness to two steviol glycosides in three species of nonhuman primates. Curr Zool 64:63–68.
193. Wielbass A et al. 2015. Gustatory responsiveness of black-and-white ruffed lemurs (*Varecia variegata variegata*) to food-associated sugars. Int J Primatol 36:460–472.
194. Purba LHPS et al. 2017. Functional characterization of the TAS2R38 bitter taste receptor for phenylthiocarbamide in colobine monkeys. Biol Lett 13:20160834.
195. Guevara EE et al. 2016. Potential arms race in the coevolution of primates and angiosperms: brazzein sweet proteins and gorilla taste receptors. Am J Phys Anthropol 161:181–185.
196. Dausch Ibañez D et al. 2019. Taste responsiveness of spider monkeys to dietary ethanol. Chem Senses 44:631–638.
197. Dudley R. 2002. Fermenting fruit and the historical ecology of ethanol ingestion: is alcoholism in modern humans an evolutionary hangover? Addict Abingdon Engl 97:381–388.
198. Remis MJ. 2006. The role of taste in food selection by African apes: implications for niche separation and overlap in tropical forests. Primates J Primatol 47:56–64.

199. Sugawara T, Imai H. 2012. Post-genome biology of primates focusing on taste perception. In: Hirai H et al., editors. *Post-Genome Biol Primates*. Tokyo: Springer. p 79–91.
200. Gochman SR et al. 2016. Alcohol discrimination and preferences in two species of nectar-feeding primate. R Soc Open Sci 3:160217.
201. Purba LHPS et al. 2020. Evolution of the bitter taste receptor TAS2R38 in colobines. Primates 61:485–494.
202. Itoigawa A et al. 2021. Lowered sensitivity of bitter taste receptors to β-glucosides in bamboo lemurs: an instance of parallel and adaptive functional decline in TAS2R16? Proc R Soc B Biol Sci 288:20210346.
203. Liu G et al. 2014. Differentiated adaptive evolution, episodic relaxation of selective constraints, and pseudogenization of umami and sweet taste genes TAS1Rs in catarrhine primates. Front Zool 11:79
204. Marzke MW. 2013. Tool making, hand morphology and fossil hominins. Philos Trans R Soc Lond B Biol Sci 368:20120414.
205. Picaud S et al. 2019. The primate model for understanding and restoring vision. Proc Natl Acad Sci 116:26280–26287.
206. Higham JP, Dominy NJ. 2018. The promise of primatology fulfilled? Am J Phys Anthropol 166:783–790.
207. Dangles O et al. 2009. Variability in sensory ecology: expanding the bridge between physiology and evolutionary biology. Q Rev Biol 84:51–74.
208. Zwolak R. 2018. How intraspecific variation in seed-dispersing animals matters for plants. Biol Rev 93:897–913.
209. Orkin JD et al. 2021. The genomics of ecological flexibility, large brains, and long lives in capuchin monkeys revealed with fecalFACS. Proc Natl Acad Sci 118:e2010632118.
210. Melin AD et al. 2014. The behavioral ecology of color vision: considering fruit conspicuity, detection distance and dietary importance. Int J Primatol 35:258–287.
211. Waszak SM et al. 2010. Systematic inference of copy-number genotypes from personal genome sequencing data reveals extensive olfactory receptor gene content diversity. PLoS Comput Biol 6:e1000988.
212. Olender T et al. 2012. Personal receptor repertoires: olfaction as a model. BMC Genomics 13:414.
213. Robin S et al. 2009. Genetic diversity of canine olfactory receptors. BMC Genomics 10:21.
214. Richgels PK, Rollmann SM. 2012. Genetic variation in odorant receptors contributes to variation in olfactory behavior in a natural population of *Drosophila melanogaster*. Chem Senses 37:229–240.
215. Trimmer C et al. 2019. Genetic variation across the human olfactory receptor repertoire alters odor perception. Proc Natl Acad Sci 116:9475–9480.
216. Kim U et al. 2006. Variation in the human *TAS1R* taste receptor genes. Chem Senses 31:599–611.
217. Hayakawa T et al. 2012. Eco-geographical diversification of bitter taste receptor genes (*TAS2Rs*) among subspecies of chimpanzees (*Pan troglodytes*). PloS One 7:e43277.
218. Suzuki-Hashido N et al. 2015. Rapid expansion of phenylthiocarbamide non-tasters among Japanese macaques. PLoS One 10:e0132016.
219. Widayati KA et al. 2019. Functional divergence of the bitter receptor TAS2R38 in Sulawesi macaques. Ecol Evol 9: 10387–10403.
220. Leat SJ et al. 2009. Development of visual acuity and contrast sensitivity in children. J Optom 2:19–26.
221. Dunn W et al. 2015. Measuring change in somatosensation across the lifespan. Am J Occup Ther 69:p1–p9.
222. Sorokowska A et al. 2015. Changes of olfactory abilities in relation to age: odor identification in more than 1400 people aged 4 to 80 years. Eur Arch Otorhinolaryngol 272:1937–1944.
223. Shively CA et al. 2021. Nonhuman primates at the intersection of aging biology, chronic disease, and health: an introduction to the American journal of primatology special issue on aging, cognitive decline, and neuropathology in nonhuman primates. Am J Primatol 83:e23309.
224. Bilkó Á et al. 1994. Transmission of food preference in the rabbit: The means of information transfer. Physiol Behav 56:907–912.
225. Schaal B et al. 2000. Human foetuses learn odours from their pregnant mother's diet. Chem Senses 25:729–737.
226. Mennella JA et al. 2001. Prenatal and postnatal flavor learning by human infants. Pediatrics 107:e88.
227. Janson CH, van Schaik CP. 1993. Ecological risk aversion in juvenile primates: slow and steady wins the race. In: Pereira ME, Fairbanks LA, editors. *Juv Primates Life Hist Dev Behav*. Chicago: University of Chicago Press. p 57–74.
228. Hoover K. 2021. *Sensory disruption and sensory inequities in the Anthropocene*. Rochester, NY: Social Science Research Network.
229. Nusbaum NJ. 1999. Aging and sensory senescence. South Med J 92:267–275.
230. Spence C, Youssef J. 2021. Aging and the (chemical) senses: implications for food behaviour amongst elderly consumers. Foods Basel Switz 10:168.
231. Aujard F, Némoz-Bertholet F. 2004. Response to urinary volatiles and chemosensory function decline with age in a prosimian primate. Physiol Behav 81:639–644.
232. Tardif SD et al. 2011. The marmoset as a model of aging and age-related diseases. ILAR J 52:54–65.
233. Henkel S, Setchell JM. 2018. Group and kin recognition via olfactory cues in chimpanzees (*Pan troglodytes*). Proc R Soc B Biol Sci 285:20181527.
234. Gray DT, Barnes CA. 2019. Experiments in macaque monkeys provide critical insights into age-associated changes in cognitive and sensory function. Proc Natl Acad Sci 116: 26247–26254.
235. Whitson HE et al. 2018. American Geriatrics Society and National Institute on Aging bench-to-bedside conference: sensory impairment and cognitive decline in older adults. J Am Geriatr Soc 66:2052–2058.
236. Fröhlich M, van Schaik CP. 2018. The function of primate multimodal communication. Anim Cogn 21:619–629.
237. Stöckl AL, Kelber A. 2019. Fuelling on the wing: sensory ecology of hawkmoth foraging. J Comp Physiol A 205:399–413.
238. Suriyampola PS et al. 2020. Reversibility of multimodal shift: zebrafish shift to olfactory cues when the visual environment changes. Integr Comp Biol 60:33–42.
239. Riffell JA. 2020. The neuroecology of insect-plant interactions: the importance of physiological state and sensory integration. Curr Opin Insect Sci 42:118–124.
240. Pijanowski BC et al. 2011. Soundscape ecology: the science of sound in the landscape. BioScience 61:203–216.
241. Quam R et al. 2015. Early hominin auditory capacities. Sci Adv 1:e1500355.
242. Houle A et al. 2014. Vertical stratification of the nutritional value of fruit: macronutrients and condensed tannins. Am J Primatol 76: 1207–1232.
243. Gould SJ, Lewontin RC. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc R Soc Lond B Biol Sci 205:581–598.
244. Kimura M. 1983. *The neutral theory of molecular evolution*. Cambridge, UK: Cambridge University Press.
245. von Cramon-Taubadel N von. 2019. Multivariate morphometrics, quantitative genetics, and neutral theory: developing a “modern synthesis” for primate evolutionary morphology. Evol Anthropol Issues News Rev 28:21–33.

246. Kamilar JM, Cooper N. 2013. Phylogenetic signal in primate behaviour, ecology and life history. Philos Trans R Soc B Biol Sci 368:20120341.

247. Hall MI et al. 2012. Eye shape and the nocturnal bottleneck of mammals. Proc R Soc B Biol Sci 279:4962–4968.

248. Kirk EC. 2004. Comparative morphology of the eye in primates. Anat Rec A Discov Mol Cell Evol Biol 281A:1095–1103.

249. Veilleux CC, Lewis RJ. 2011. Effects of habitat light intensity on mammalian eye shape. Anat Rec 2007 294:905–914.

250. Hiramatsu C et al. 2017. Experimental evidence that primate trichromacy is well suited for detecting primate social colour signals. Proc R Soc B 284:20162458.

251. Santos PSC et al. 2010. Genomic architecture of MHC-linked odorant receptor gene repertoires among 16 vertebrate species. Immunogenetics 62:569–584.

252. Secundo L et al. 2015. Individual olfactory perception reveals meaningful nonolfactory genetic information. Proc Nat Acad Sci USA 112:8750–8755.

253. Santos PSC et al. 2018. The best smellers make the best choosers: mate choice is affected by female chemosensory receptor gene diversity in a mammal. Proc R Soc B 285:20182426.

254. Jacobs RL, Bradley BJ. 2016. Considering the influence of nonadaptive evolution on primate color vision. PLoS One 11:e0149664.

255. McGann JP. 2017. Poor human olfaction is a 19th-century myth. Science 356:eaam7263

256. Mollon JD. 1989. "Tho' she kneel'd in that place where they grew…" The uses and origins of primate colour vision. J Exp Biol 146:21–38.

257. Martin RD, Ross CF. 2005. The evolutionary and ecological context of primate vision. In: Kremers J, editor. *Primate Vis Syst*. John Wiley & Sons, Ltd. p 1–36.

AUTHOR BIOGRAPHIES

Carrie C. Veilleux is an assistant professor in the Anatomy Department at Midwestern University in Glendale, Arizona. Her research is focused on investigating the ecological factors that influence intraspecific and interspecific variation in the sensory systems of primates and other mammals.

Nathaniel J. Dominy is the Charles Hansen Professor of Anthropology at Dartmouth College. His research program is focused on the functional anatomy and feeding ecology of humans and nonhuman primates in tropical habitats.

Amanda D. Melin is an associate professor and Canada Research Chair in the Department of Anthropology & Archaeology and Medical Genetics at the University of Calgary, AB. She also co-directs the Santa Rosa Primate Project. She studies the molecular, behavioral, and dietary ecology of primates and other mammals to understand how sensory systems evolve.

How to cite this article: Veilleux CC, Dominy NJ, Melin AD. The sensory ecology of primate food perception, revisited. Evolutionary Anthropology. 2022;31:281-301. doi:10.1002/evan.21967