

THE FORAGING STRATEGIES OF PRIMATES

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Summary

There are between 200 and 300 living primate species. Primates mainly inhabit lowland tropical rain forests in South East Asia, Madagascar, Africa and Central and South America. This habitat is that in which they are most diverse, and they often dominate the arboreal animal biomass in such forests. The largest living arboreal mammal, the orangutan, is a primate. Field studies show that the diets of primates are not stereotyped, but vary greatly through the year depending on the availability of food items that are rarely abundant. Ripe fruits are the major food source, but are subject to competition from other animals. There is therefore, considerable selective pressure on primates to detect such food sources before their competitors do. Variation in many of the important senses of primates used in foraging can be understood in this light. There are two important trends in the primate visual system relevant to feeding strategies: binocularity, which involves the overlap of right and left visual fields, and color vision. Trends in olfaction, which has often been thought to have been reduced in significance during primate evolution, are also relevant and are lesser-known areas such as tactile sensitivity. Despite their apparent dietary flexibility, primates are not indiscriminate feeders, suggesting that there are important behavioral 'rules' to discover that may underlie their foraging strategies. Conventional views of optimal foraging tend to explain behavior in terms of energy budgets and nutritional requirements. However, it is not at all clear that even humans, as members of the primate order, have any internal mechanisms for relating their nutritional and energy requirements directly to food items placed in front of them. If there were, 'fad' diets would be unlikely to exist. Thus, the objective of this chapter is to lay out a case for sensory ecology, considering what the

senses can relate to a primate about potential foods, and the internal signaling that may result from what they convey.

1. Introduction

Faced with the complex scenery of a tropical rainforest, the environment in which most primate species live, how does a primate decide what objects might be potential foods and what just constitutes their scenic setting: their foreground and backcloth? The answer must surely be that a primate individual uses its senses to identify such objects, variously judging their edibility by their size, shape, color, smell, texture and taste. Not all these attributes are perceivable at different distances. For example, it is difficult for an animal to see very far in a rainforest because leaves get in the way. And any animal needs to at least touch an object in order to sense its texture and, further to bite into it before any taste is released. Accordingly, a primate is likely to be led towards a potential food object by a chain of positive **sensory cues**, some of which act at longer distances than others. At any point along that chain, the animal may reject the object.

Of course, no primate has to make instant decisions informed only by what its senses tell it. Social and individual learning are involved and the interpretation of such cues must depend strongly on its memory. A primate may be able to associate object attributes with a feeling of well-being from consuming them previously. However, so far all of this really only describes what may pass when a primate has already identified things that could be eaten and can then home in on them. There is a problem though for primates in even getting into their vicinity (a region defined as one in which its senses can act), because primates eat food items that are not continuously available. Although many primates, particularly the smallest, are insectivorous, we know more about the seasonality of plant foods than of insects. The primate order as a whole is in fact largely vegetarian, the larger members being almost exclusively so.

Though wood forms the bulk of the plant biomass, no primate eats it. Indeed primates select against the ingestion of woody 'fiber', probably by using the textural cue of toughness. They tend not to eat mature foliage, which can be very woody and tough. Though bark is eaten by some primates, it is generally not a staple. Instead, primates target plant items that are only seasonally available, such as ripe fruits or young, immature leaves. The descriptive terms 'ripe', 'young' and 'immature' here are obviously subjectively defined by human observers. There is no evidence that primates continually monitor fruits or leaves and thus it is difficult to believe that they make estimates of the age of these items. Instead, variables like size, color and smell must be all-important. The sum of all this is that we cannot simply state that the foraging strategy of a primate is designed around (say) the consumption of the fruits of species x or the leaves of species y . For much of the period of development of such fruits and leaves, a timeframe that might be weeks or months, the primate may simply ignore them. So what we have to work towards is the definition of a food item in terms of the mental model that a primate might have of them. This is the aim of sensory ecology, a relatively new way to think about foraging strategies. It may differ strongly from a perspective based on energetics, or nutrition, depending on how closely connected sensory perceptions are to nutritive requirements. Obviously, the animal is built to survive, but the 'slack' between what the senses can convey to an animal and what

would constitute its best nutritional choice can be very revealing about what drives foraging choices.

2. The Senses of Primates

Due to the seasonal nature of plant resources, it can be hard for a primate even to get into their vicinity where its senses could act. To help, it is clear that members of primate species, along with many other animals, can create maps of their environment. This mapping ability acts in a way as an extra sense, allowing a primate to remember locations of potential foods. Once a primate knows that a certain fruit is becoming a food, it can use its memory to locate many other trees. There is evidence that primates can maneuver rapidly through forests without deviating much from a straight line between neighboring trees. This saves them from a random walk, which generally halves the distance that a primate could cover in a given time period. Present evidence suggests that the 'remembered space' of a primate may be equal to the size of its **home range**, i.e. it always knows where it is. In contrast, the senses of primates, as conventionally described, often do not carry very far. Food calls and noises associated with feeding by other animals (e.g. the dropping of fruit parts), can be very effective methods of finding food resources by hearing. Calls may carry up to 2 km in what is often a very quiet environment. The next in distance is probably smell. Low molecular weight volatiles may waft as far as 200 m from their source, though there have been few field studies on this. Despite the visual system having key enhancements in primates, it is difficult for them to see far in the forest canopy because leaves get in the way, even just a meter or so from their faces. Key factors here, as in all these sensory considerations, are the size of the animal, which has a large impact on its home range, and in particular for the visual system, the spacing between its left and right eyes. Experimental evidence in New World capuchins of around 2-3 kg in body weight suggest that 20-30 m may be the farthest that they can see. Despite these limitations, there have been more investigations of primate vision in relation to foraging than any other sense. At shorter-distances, the next most important sense is that of touch, the boundary of which extends only to 'arm's length'. Touch can provide information on a whole group of attributes that can be listed under texture. Textural perceptions involving the hand include surface features and also the deformability of the food object. These evaluations can then be enhanced by taking them into the mouth and biting into them with the teeth. Lastly, biting releases fluids in the food leading to sensations of taste. Like that of smell, our understanding of tastes has gone through something of a revolution in understanding in the last decade of the 20th Century.

3. Vision in Primates

More is known about the role of vision in primate foraging than of any other sense. We humans generally say that vision is our most salient sense, i.e. that it gives us more information about our surroundings than any other. We use it to recognize objects by many characteristics including their position, form and surface texture. We can tell whether these objects are close by or far away and we can assign colors to them from a range of more than six million different hues (though we don't have specific color names for very many of these). Other primates share these abilities to some extent and have a lot of uses for them, including in foraging. There are two distinct trends seen

within the order: a tendency towards binocularity and a trend towards color enhancement.

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Biographical Sketch

Peter W. Lucas received a B.Sc. Hons degree from University College London in 1976, and Ph.D. and D.Sc. degrees from the University of London in 1980 and 2002 respectively. He has been a faculty member at the National University of Singapore, the University of Hong Kong and is currently Professor of Anthropology at the George Washington University in Washington DC. He is a member of the American Association of Physical Anthropologists. His interests centre on the function and evolution of the mouth in humans, primates and other mammals. This has broadened from an initial focus on dental

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