



The interplay between individual, social, and environmental influences on chimpanzee food choices



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ABSTRACT

The foraging activity of chimpanzees requires individuals to balance personal preferences with nutrient requirements, food availability, and interactions with members of their social group. To determine whether chimpanzee food preferences are fixed or malleable across varying socio-ecological contexts, we presented six zoo-housed chimpanzees with pairwise combinations of four different foods under two experimental conditions. First, we individually tested each chimpanzee's choices for the four foods to ascertain individual preferences. Second, we tested the chimpanzees in a situation which more-closely mimicked the foraging pressures experienced by wild chimpanzees. In this second condition, the chimpanzees were tested in a group setting and the food availability was less predictable, such as in a patchy foraging environment. Subjects expressed significant variation in their selection of which foods to consume in the two different contexts and also appeared more willing to consume less-preferred foods in the unpredictable, social environment. These results suggest that chimpanzees' food preferences are not fixed, but change with context and are likely mediated by social facilitation. This is not only important to understand chimpanzees' foraging patterns and dietary requirements, but also has implications for experimental paradigms that rely on food preferences.

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1. Introduction

Does what we choose to eat, reflect what we prefer to eat? For humans, such choices are influenced as much from a nutritional standpoint, as from a social-psychological perspective (Pliner and Mann, 2004). In contrast, the food choices of nonhuman animals have classically been studied within an ecological framework with an aim to understand how animals forage most effectively given the environmental pressures they face (e.g., Bates and Byrne, 2009; Duffy and Hay, 1991; Janmaat et al., 2006; Janson, 1998; Sih, 1982; Torres-Contreras and Bozinovic, 1997). Less import is given to how social and environmental pressures interact, and whether they impact food preferences and food choices. This is particularly surprising when considering chimpanzees (*Pan troglodytes*), which are a highly gregarious nonhuman primate species that have a complex, omnivorous diet.

In the wild, chimpanzees spend 40–60% of their active time feeding (Wrangham, 1977) yet they consume only a small portion of available food items (Sugiyama and Koman, 1987; Wrangham, 1977). Chimpanzees are constantly making choices about what foods to eat, but are their foraging choices dictated primarily by personal preference? Models of primate socioecology suggest that chimpanzee foraging behavior is guided by a complex interplay between food availability, food choices, group composition, and location (Wrangham, 1980; Isbell, 1991). Furthermore, primate behavior and foraging is heavily shaped by periods of food shortages, during which rare but preferred foods and low-value 'fallback' foods become especially important (Marshall and Wrangham, 2007; Rosenberger, 2013). Thus, it is presumed that social and environmental influence interact to affect food choices, but there is little data from controlled experiments to validate these predictions.

It might be assumed that animals preferentially select those foods that are nutritionally beneficial for them (e.g., Carlson et al., 2013), or that they would select those foods that are easy to obtain, the proverbial 'low hanging fruit' (Koops et al., 2013). However, a number of species will travel considerable distances when foraging (e.g., *Apis mellifera*, Beekman and Ratnieks, 2000; *Ateles geoffroyi*

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yucatanensis, Valero and Byrne, 2007). Furthermore, even when nutritionally-appropriate foods are readily available, animals still do not always select them (Forbes and Kyriazakis, 1995; Sousa and Matsuzawa, 2006; Yeomans et al., 2004). Potentially 'healthy' foods are overlooked in preference for foods that are more palatable. Chimpanzees, for example, appear to use sugar content (Wrangham et al., 1998; Remis, 2002, 2006) and energy yields (Matsumoto-Oda and Hayashi, 1999) to guide their food selection, but both texture and taste have also been shown to be factors that primates use to assess food quality (Remis, 2002).

In addition to the physical properties of the food itself, primate foraging patterns may also be affected by social influences (e.g., *Papio cynocephalus*, Alberts et al., 1996). Chimpanzees forage with members of their social group (Nishida, 1968) and rarely encounter food sources alone. Thus, social environment may affect individual food choice (Hopper et al., 2011; Lonsdorf and Bonnie, 2010, but see van Leeuwen et al., 2013). Synchronization of feeding activities can result in competition for food (Oates, 1987) and chimpanzees show contest-type competition (Wittig and Boesch, 2003). Consequently, low-ranking females, and other subordinates, tend to have a lower quality diet, and forage less efficiently, than higher-ranking female chimpanzees (Murray et al., 2006; Parish, 1994). In this way, the pressures of group living can directly impact which foods an individual chooses to eat, regardless of personal preference.

The impact of a chimpanzee's social group on foraging patterns may also arise through social facilitation. Like for humans, who have been shown to develop preferences for foods that are liked by their family, peers, or esteemed individuals (Birch, 1980; Duncker, 1938; Pliner and Pelchat, 1986; but see Pliner and Mann, 2004), there is emerging evidence that chimpanzees may choose to eat foods that a dominant animal selects, even if it is not their preferred food (Hopper et al., 2011, see also Galef and Whiskin, 2008; Sherwin et al., 2002; van de Waal et al., 2013, for comparable data with other species). But social facilitation does not only manifest through copying the food choices of others; observing a group member eating can also encourage the consumption of a different food (i.e., eating behaviors generally increase). There is evidence that social facilitation can drive capuchins to select novel or less preferred foods when observing a group member eat, regardless of the food type eaten by the demonstrator (Visalberghi and Addessi, 2000; Addessi and Visalberghi, 2001; Dindo and de Waal, 2007) and similar responses have been reported for chimpanzees (Hopper et al., 2011, but see Addessi and Visalberghi, 2006; van Leeuwen et al., 2013). Such results suggest that although an animals' preference may be constant (Visalberghi et al., 2003), it is still possible that their choices may vary according to their social environment. Importantly, and depending on the relationship an individual has with those animals present at a feeding site, the social environment may inhibit the individual's consumption (i.e., due to competition) or induce greater consumption (i.e., due to social facilitation) of certain food items. When testing food choices, therefore, it is important to consider the interaction between the individual and the social environment in which it feeds (Galef, 1996).

In addition to being of theoretical interest, an understanding of what drives individual preferences and choice is important for a number of applied reasons. For example, an understanding of what dictates animal food choices and preferences can enable us to provide better husbandry and care in a captive environment (e.g., Clay et al., 2009; Gaalema et al., 2011) and may provide insight on food availability requirements when reintroducing chimpanzees into the wild. Additionally, food preference tests form the basis of many behavioral and cognitive tests with chimpanzees (e.g., Brosnan et al., 2005; Slocombe and Zuberbühler, 2006) and understanding whether 'choice' reflects 'preference' would provide greater context for such research.

Our aim was to distinguish between chimpanzees' food preferences and food choices in differing social environments. To determine individual food preferences for four different foods we tested the chimpanzees individually ('individual' condition). In this condition, the foods that the chimpanzees had to choose between were clearly visible and the chimpanzee was afforded time to make their selection with no social pressures. In the wild, in a patchy environment, food sources may be less predictable (Houle et al., 2007), foods may require more processing, cognition, and behavioral flexibility to obtain (Milton, 1981; Lonsdorf, 2005), and individual chimpanzee's foraging strategies may be dictated by their group's (Lehmann and Boesch, 2002). To reflect this naturalistic foraging context, the second condition increased both the social and environmental pressures. We gave the same chimpanzees the same four foods, also through a series of pair-wise choices, but presented via an artificial termite mound and the chimpanzees were tested in their familiar social group ('social' condition).

Investigating food selection in these two contexts is important for detecting factors that influence group-level food choice that may be diluted or absent when individuals are tested in solitary conditions. We predicted that individual food choices would change across experimental conditions (the individual, stable, condition versus the social, unpredictable, condition) however we made no directional predictions as to how these choices would be expressed (accordingly, all analysis was two-tailed). As social pressure might affect the foraging choices of animals differentially, we also wished to determine if any differences in food choice between the conditions reflected a group-wide shift or merely a change in choices by only certain group members. To test this, we considered the chimpanzees' selections at both the individual- and group-level. This allowed us to evaluate the extent to which social, individual and environmental factors drive the chimpanzees' choices in each condition. Furthermore, in the social condition, we also analyzed whether an individual's food selection was related to the number of group mates concurrently at the mound.

2. Methods

2.1. Ethical note

This study was approved by the Lincoln Park Zoo Research Committee, which is the governing body for all animal research at the institution. No social group manipulations occurred as the result of this project and animal separations were always voluntary on the part of the apes. Food substances, amount and frequency were reviewed and approved by veterinary and nutrition staff prior to the start of the project. No modifications were made to standard animal care routines. This research adhered to legal requirements in the United States of America and to the American Society of Primatologists Principles for the Ethical Treatment of Non-human Primates.

2.2. Subjects and housing

The subjects were six captive-born chimpanzees housed together at the Regenstein Center for African Apes (RCAA) at the Lincoln Park Zoo (Chicago, Illinois, U.S.A). The group included two males and four females (average age: 17.3 years, range: 11–26 years). These chimpanzees inhabited an expansive indoor/outdoor exhibit that included climbing structures and deep-mulch bedding and an off-exhibit holding area (details below). Throughout the study, the chimpanzees had outdoor access when weather conditions were appropriate (>4.5 °C). Fresh produce and primate chow were scattered twice daily throughout their exhibits. The exhibit space housing these subjects features an artificial termite mound

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