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Food Neophobia in Rhesus macaques (Macaca mulatta)
(Under the direction of DOROTHY M. FRAGASZY)

Food neophobia can be observed in most animals and may play a key role in diet selection, especially for generalist species. This project contains five experiments aimed at elucidating the role of food neophobia in the feeding behavior of rhesus macaques (Macaca mulatta). Of primary interest was whether the macaques' behavior matched predictions derived from the hypothesis that food neophobia develops after repeated experiences of conditioned taste aversion (CTA) with novel foods. In a variety of experimental conditions, the observer recorded how long subjects manipulated novel and familiar foods, the frequency of sniffs, and whether food was eaten or dropped at the end of a trial. Food neophobia increased predictably in semi-free ranging macaques with increasing food novelty. As expected, this pattern did not hold in corral-housed animals. The source of food was important, as subjects were more likely to drop novel foods they discovered in their environment compared to those hand-tossed to them by a human observer. Macaques, as young as 1-year old, exhibited food neophobia. This result does not support the CTA hypothesis, but studies with younger infants are warranted. Pilot data on 6-month old macaques indicate that social cues from group members may influence infants' behavior toward novel food.

INDEX WORDS: Neophobia, Rhesus macaques, Feeding, Diet selection

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by

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CHAPTER 1: INTRODUCTION

Food neophobia is inferred from behavior observed in a variety of animals including humans (e.g. Domjan, 1977). The behavior is usually measured as an individual's latency to eat a novel food or as the relative amounts of novel and familiar food ingested. Many species exhibit dietary neophobia and it has been established as an important factor in diet selection for Norway rats (Galef, 1993) and livestock (Chapple & Lynch, 1986; Chapple & Wodzicka-Tomaszewska, 1987; Provenza & Balph, 1988). Comparable data for non-human primates, however, are lacking.

As habitat continues to be destroyed and altered, the management of wild and translocated populations becomes crucial to the survival of many primate species. Evidence from translocated groups indicates that monkeys typically do not immediately eat unfamiliar foods in their new location (Kawai, 1960; Biswas, Medhi, & Mohnot, 1996; but for contrary accounts see Fedigan, 1991; Silver & Ostro, 1996). It is no longer sufficient to rely on generalizations based on data from distantly related species. To gain knowledge about food neophobia with respect to primate conservation, data are needed from non-human primates. This dissertation evaluated a hypothesis regarding how neophobia might influence food selection in rhesus macaques (Macaca mulatta).

The hypothesis presented here is that food neophobia develops in dietary generalists after multiple experiences with conditioned taste aversion (CTA). Dietary generalists are species that include a greater variety of foods in their diet compared to closely related species. CTA is a distinct type of learning where a single pairing of gastrointestinal illness with an ingested item, even when ingested hours before the onset of illness, results in an aversion to that item (Garcia & Koelling, 1966; Kalat & Rozin, 1973; Richter, 1953; Rozin & Kalat, 1971). CTA is especially strong for novel edibles (Domjan, 1977; Revusky & Bedarf, 1967) and CTA for one flavor can enhance an individual's neophobia for other novel flavors (Best & Batson, 1977; Carroll, Dinc, Levy, & Smith, 1975; Domjan, 1975; Franchina & Fitzgerald, 1983; Richter, 1953; Robbins, 1980). Rozin (1976) suggested that CTA is an adaptive specialization for omnivores (dietary generalists) that, compared to dietary specialists, face increased risks in recognizing and selecting nutritious and safe food items. It is suggested here that for animals with a generalist diet, CTA is the mechanism by which food neophobia *is initially acquired*. This hypothesis is congruent with one proposed by Booth, Lovett, and McSherry (1972) who suggest that "all the normal control of dietary selection and hence of cumulative food intake in omnivorous animals such as rodents and primates was acquired by associative learning from the ordinary nutritional consequences of ingestion" (Booth, 1996, p. 39). Additionally, though food neophobia was thought to be an instinctive behavior (Barnett, 1963), weanling rats do not show neophobia to a novel flavor but young-adult and old-age rats do (Kalat & Rozin, 1973; Misanin, Blatt, & Hinderliter, 1985). These observations might reflect differences in ontogeny, but they also allow for the possibility that food neophobia is a learned behavior.

This CTA hypothesis explains the development of food neophobia as follows: when a young rhesus macaque (an omnivorous species) begins to forage independently, it will ingest items that may or may not be suitable food. The monkey will gradually become familiar with foods that are safe to eat and fulfill its nutritional requirements. Toxic items ingested will produce illness and the animal will develop a conditioned taste aversion (CTA) to those items. After enough experiences with items that produce CTA, a monkey, in addition to avoiding those particular items, will exhibit stimulus generalization based on novelty.

Stimulus generalization based on novelty can be observed in rats with a phenomenon called poison-enhanced neophobia. Domjan (1975) found that rats that had acquired an aversion to sucrose expressed greater then normal neophobia toward a novel vinegar or casein solution. When Best and Batson (1977) paired toxicosis with exposure to a novel coffee solution, rats again showed enhanced neophobia to a novel vinegar and a novel casein solution. Carroll et al. (1975) and Franchina and Fitzgerald (1983) also reported that, in rats, toxicosis paired with a flavor produced enhanced neophobia to other novel flavors. I propose that a dietary generalist primate may also develop a cautious approach toward items based on their novelty and this is what we observe as food neophobia.

Several predictions follow from the proposed CTA hypothesis. A primate that has not had the requisite experience with CTA should not exhibit food neophobia. Young primates and captive adult primates are a good illustration. Young individuals from several primate species (tufted capuchins: Fragaszy, Visalberghi, & Galloway, 1997; baboons: King, 1994; langurs: Poirier, 1970; vervet monkeys: Struhsaker, 1967; marmosets: Vitale & Queyras, 1997) have shown themselves to be either less neophobic than adults or willing to eat items that adults of their species apparently never ingest. Though young animals are commonly thought to explore and investigate more than adults (Box, 1984; Menzel, 1966), in the case of food, their lack of caution might be explained as a failure to have yet developed the species-typical adult trait of food neophobia.

Captive primates may have little or no CTA experience because they receive only palatable food from humans. This might explain the apparent lack of neophobia observed in some adult primates under captive conditions (person. observ.).

It could also be expected that food neophobia may be modified according to the principles governing associative learning. Food neophobia is thought to be a strategy that protects animals from ingesting unknown and possibly harmful substances (for general theory see Domjan, 1977; Rozin, 1976; for primates see Glander, 1981; Hladik & Simmen, 1997; Visalberghi, 1996). Any stimulus that acts as a learned safety signal that a potential food is safe should circumvent neophobic behavior.

Rozin (1976) and Galef (1991) both point out that most naturally occurring toxins are bitter tasting. Sweet substances, on the other hand, usually have many calories and are a good source of energy. Indeed many primate species are important seed dispersers for fruit bearing plants, and some plant species are specially adapted to produce fruits that attract non-human primates as dispersal agents (Stiles, 1989). Fruits that have evolved to be attractive for their dispersal agents do not contain high levels of aversive or illness-inducing substances (Robbins, 1983). Therefore, it is probably rare for naturally occurring sweet substances to be paired with illness after ingestion. Booth et al. (1972) found that post-ingestive effects other than illness can alter dietary preferences. They report that, contrary to their initial preference, rats came to prefer a less sweet solution that contained glucose and other carbohydrates (Booth et al., 1972). Just as pairing taste with illness may prevent eating a food in the future, experience with a taste that reduces hunger and does not cause illness, such as a sweet taste, may increase the likelihood that that food will be eaten again and accepted rapidly. Sugar-containing foods are highly preferred by primates (Simmen & Hladik, 1998; Steiner & Glaser, 1984). The sugar content of a new food might act as a learned safety signal so that animals that normally exhibit food neophobia would not do so if the novel food is sweet as opposed to bitter tasting.

Support for this prediction comes from Whitehead's (1986) observations of two mother-infant pairs of mantled howler monkeys (Alouatta palliata). He found that when foraging on new foods, the infants exhibited behavior consistent with socially dependent feeding processes when feeding on new leaf species. The infants looked at their mothers before feeding, adopted the same posture, and even ate from the same branch as their mothers (Whitehead, 1986). In contrast, when feeding on fruits the infants' behavior appeared to be socially independent. Whitehead (1986) suggested the infants' conservative behavior with new leaf species reflects the importance of choosing items selectively from potentially toxic leaves, while fruit trees have co-evolved with primate seed dispersers and present little or no danger to the young animals.

Humans may become a learned safety signal for animals that are directly provisioned by them. Direct provisioning entails the opportunity to learn that humans are associated with food, in contrast to indirect provisioning or commensalism, as happens when animals scavenge from dumps. Though it may be difficult to observe food neophobia in captive primates that live in relatively sterile environments, a provisioned animal living in a natural environment would still have the opportunity to ingest harmful items and experience CTA. Under these conditions it might be expected that an animal might both develop food neophobia and associate humans with palatable food. Human provisioning would act as a learned safety signal, just as sugar content might. It would be expected that animals living in a natural environment would show neophobia to items they find in their environment but not be neophobic toward items given to them by humans. Watanabe (1989) described Japanese monkeys (Macaca fuscata) living in public parks that, after years of receiving handouts from human visitors, no longer hesitate to eat items given to them by humans. Surely some of these items are new to some of the monkeys some of the time and in other contexts would elicit a neophobic response. This supports the hypothesis that humans may serve as a learned safety signal for provisioned animals, eliminating the need for neophobic behavior toward items provided by humans.

Provisioned rhesus macaques living in an intact natural environment are an excellent population in which to address the questions raised here. A previous study with such a population found that food neophobia is easily described and quantified and is robust even during periods of extreme food shortage. Free ranging rhesus macaques manipulated novel foods longer, sniffed them more frequently, and were more likely to drop, therefore reject, a novel food compared to a familiar food (Johnson, 2000). These behaviors did not change even after the monkeys' regular provisioning was withheld for periods ranging from 14 to 84 hours (Johnson, 2000).

These same behaviors were measured in the present experiments and chosen for the following reasons. Manipulation and sniffing are typical exploratory behaviors and can be expected to occur while a monkey is deciding whether or not to ingest a novel food. Hesitation to eat a novel food is expressed as the duration of manipulation. Sniffing was deemed particularly important because it is the first thing rhesus macaques do upon picking up a novel food (person. observ.) Whether food was dropped or eaten is the most direct measure of the decision an individual subject makes while food is manipulated, sniffed, and tasted.

This dissertation contains five experiments that further investigate food neophobia in the same population of rhesus macaques described above. Experiment one is designed to investigate whether a change in the appearance or odor of a food may elicit food neophobia. The implication is that appearance and odor are stimulus properties macaques use to distinguish an item as a familiar or novel food. Franchina, Johnson, and Leynes (1994) found a similar result in domestic chicks where increases in the concentration of red food coloring in their novel test solution caused increases in the chicks' latency to drink the solution.

In experiment two, the difference between the neophobic response of island monkeys is compared to that of rhesus macaques raised and housed in corrals. Because corral-raised animals have little opportunity to experience CTA, they are expected to exhibit no neophobic response toward the same food that elicits neophobia in the island monkeys.

Experiment three is designed to test whether provisioning by humans acts as a learned safety signal. It is expected that provisioned monkeys who live in an intact habitat will display neophobia when encountering a novel food found in the environment but will not be neophobic when given a novel food by a human.

In experiment four, food neophobia is measured in macaques of different ages. If food neophobia is learned, then young animals should not exhibit food neophobia or should do so to a lesser degree than adults.

Finally, experiment five is designed to show a relationship between palatability and neophobia. If sugar content acts as a safety signal, then sugar-containing novel food should not elicit neophobia.

These five experiments were used to test whether aspects of food neophobia in rhesus macaques are consistent with predictions derived from the CTA hypothesis. The results may provide a better understanding of diet selection in a generalist primate species and may ultimately aid efforts to manage wild primate populations.

CHAPTER 2: METHODS & RESULTS

Methods for Experiment One: Visual & Odor Cues

Subjects and Study Site

The subjects for experiment one were 60 male and 60 female rhesus macaques aged five years or older. The monkeys were part of a breeding colony of about 2400 animals that range freely on a small island operated by Laboratory Animal Breeders & Services (LABS) of Virginia, Inc. off the coast of South Carolina. The colony is provisioned daily with commercial laboratory chow and fresh water. Though this provisioning constitutes the staple of the monkeys' diet, they also forage on island vegetation (e.g. acorns, pine cones, soil, mushrooms, green leaves, green pine needles). The semi-tropical climate supports a mixed evergreen forest, dominated by live oak, and is surrounded by salt marsh. The animals were tattooed, allowing individual identification. Subjects for all the following experiments, except experiment two, came from this colony.

Procedure

The experimenter hand-tossed subjects one of four test foods. Test foods included half a monkey chow biscuit that was (a) unaltered (familiar looking and smelling), (b) dyed with red food coloring (novel looking), (c) treated with lemon food flavoring (novel smelling), or (d) treated both with red food coloring and lemon flavoring (both novel looking and smelling). Red chow was prepared by dipping chow pieces in a solution of about 200 ml water with 10 ml of red food coloring. The chow was then baked at 300 degrees for 20 to 30 minutes to restore hardness. Novel smelling chow was prepared by using a piece of wire mesh to suspend chow pieces over 10 ml of lemon food flavoring in a closed 300 cm^3 plastic container overnight.

Fifteen male and fifteen female subjects were chosen opportunistically for each condition as the experimenter walked around the island. The experimenter recorded on audio-tape every time the subject touched, picked-up, sniffed, tasted, ate, or dropped a piece of food. The trial began when a subject first touched or sniffed the test food and ended when the subject dropped or ate the test food with no further behavior directed toward the test food for 10 seconds. Two observers recorded practice data for 16 trials with corral living rhesus macaques. The observers recorded 112 behaviors (pick, sniff, taste, eat, and drop) and agreed on 106 of these (95% agreement). The observers recorded trial durations that differed an average of .87 seconds (calculated from eight of the sample trials). One of these observers then conducted the experiments.

Three dependent variables were measured from the audiotape: (a) the total length of time the subject handled the food (manipulation time), (b) the number of sniffs directed toward the food, and (c) whether the animal ultimately dropped or ate the food piece. The variable "drop" versus "eat" actually refers to the fate of the last bit of food regardless of whether the monkey ingested or spit out pieces of food earlier in the trial.

This procedure of recording food-directed behavior was used in all five experiments. Neophobia was inferred when, compared to a familiar food, monkeys manipulated novel food longer, sniffed it more frequently, or were more likely to drop it at the end of the trial. It was expected that subjects would be neophobic toward test foods that were novel in appearance, odor, or both.

There was no a priori reason for expecting one of the dependent variables to be more important than the others when interpreting the results. Arguably, the alpha level should be adjusted to reflect the fact that multiple measures were used to test for food neophobia. An alpha level of $\propto < .017$ would be appropriate according to the Bonferroni method. For the purposes of the present discussion however, $\propto < .05$ was retained as the criterion for significance while acknowledging multiple measures were used. A meta-analysis of the hypotheses tested (presented below) supports this decision.

Results for Experiment One

Analysis of variance (ANOVA) was used to analyze manipulation time and the frequency of sniffs in all experiments. Due to heteroskedasticity, the frequency of sniffs was transformed by taking the square root to normalize the data. Chi Square tests of homogeneity were used to analyze the number of drops versus eats observed in each experiment. .

Analyses of variance found no main effect of food type or sex on manipulation time. The monkeys handled all test foods for similar durations ($\underline{M}_{\text{unaltered}} = 59.03$, $\underline{M}_{\text{red}} = 54.13$, $\underline{M}_{\text{lemon}} = 66.00$, $\underline{M}_{\text{red/lemon}} = 66.63$ seconds). Neither sex nor food type affected the frequency of sniffs directed toward food pieces ($\underline{M}_{\text{unaltered}} = 4.93$, $\underline{M}_{\text{red}} = 6.83$, $\underline{M}_{\text{lemon}} = 7.23$, $\underline{M}_{\text{red/lemon}} = 7.93$ sniffs).

Sixteen of the 120 subjects in experiment one participated in two or more experiments on food neophobia. In post hoc tests, data from these subjects were eliminated from the analysis to test whether they biased the data. Five subjects were dropped from the unaltered chow condition, five from the red chow condition, four from the lemon chow condition, and two from the red/lemon chow condition. After dropping these subjects the differences in manipulation time and sniffs remained equivalent (F (1, 99) = 2.552, p = .06 for sniffs). The sample means for the number of sniffs was in the direction predicted for neophobia in that unaltered chow was sniffed the least (M = 4.9), red chow and lemon chow were sniffed at similar rates (M = 6.8, M = 7.2), and red/lemon chow was sniffed the most (M = 7.9).

A Chi-square test found that whether or not food was dropped depended on food type (χ^2 (1, N = 120) = 7.939, p = .047, Figure 1). Again the data were in the direction predicted in that unaltered chow was dropped the least (8 trials), red chow and lemon chow were dropped at similar rates (11 trials for red and 10 trials for lemon), and red/lemon chow was dropped most often (18 trials). There was no difference between the number of drops observed for males and females.

Methods for Experiment Two: Corral-housed Macaques

Subjects

Subjects were 23 male and 37 female rhesus macaques that were raised and continued to live in outdoor corrals at the Yemassee facility of LABS of Virginia, Inc. Each corral consisted of two open enclosures, each measuring approximately 30 x 15 meters, connected by two small guillotine doors that provided access to both sides of the corral. Each enclosure had large, wooden climbing structures, a 2 x 2 meter covered bin of monkey chow, a water pipe with two drinking nozzles, and a dirt or gravel floor. The number of subjects used was constrained by the fact that only two to four adult males were housed in each group with group sizes ranging from 50 to 100 animals. Also, in this setting, dominant individuals prevented other group members from receiving food that was tossed into the corral.

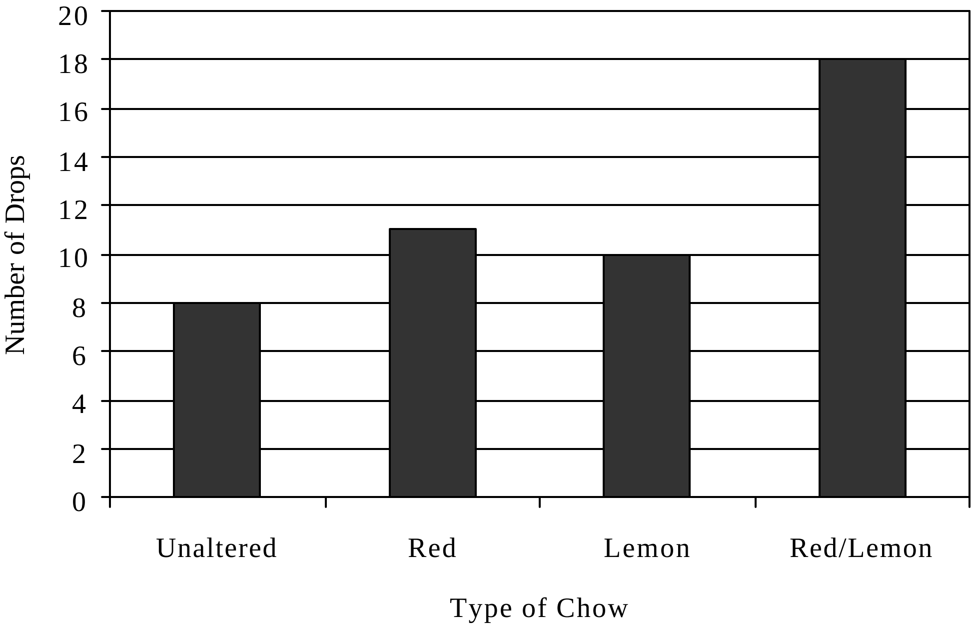

Figure 1. Number of drops observed in island-living rhesus macaques.

Procedure

Subjects were hand-tossed either half a regular chow biscuit or half a novel looking and smelling chow biscuit (red/lemon), as described in experiment one. It was expected that the food-directed behavior of corral-living animals would not differ for novel and familiar foods and that this pattern would be different from that observed in island-living macaques.

Results for Experiment Two

An ANOVA on data from corral-housed monkeys indicated that neither sex nor food type had an effect on manipulation time. However, post hoc t-tests found that corral monkeys manipulated novel foods significantly less than island monkeys ($\underline{M}_{\text{corral}} = 40.4$, $\underline{M}_{\text{island}} = 66.6$ seconds; $\underline{t}(58) = 2.083$, $\underline{p} = .04$) while familiar foods were manipulated for similar durations in the two groups.

Food type did not affect the frequency of sniffs directed toward food. Sex affected the frequency of sniffs as corral-housed females sniffed food less often than males ($\underline{M}_{\text{females}} = 1.56$, $\underline{M}_{\text{males}} = 2.13$ sniffs; $\underline{F}$ (1, 59) = 4.26, $\underline{p} = .0437$). There was no interaction between sex and food type. Post-hoc analyses showed that corral monkeys sniffed novel chow less often than island monkeys did ($\underline{t}(58) = 3.67$, $\underline{p} = .001$) but the two groups sniffed plain chow similarly.

Chi-square tests found no relationship between sex and the likelihood that food was dropped or between food type and the number of drops. Moreover, the pattern of drops was opposite to that expected for neophobia as subjects dropped familiar food on 16 of 30 trials and dropped novel food on 9 of 30 trials (χ^2 (1, $\underline{N} = 60$) = 3.36, $\underline{p} = .067$, Figure 2). Post-hoc analyses found that corral monkeys dropped plain chow more often

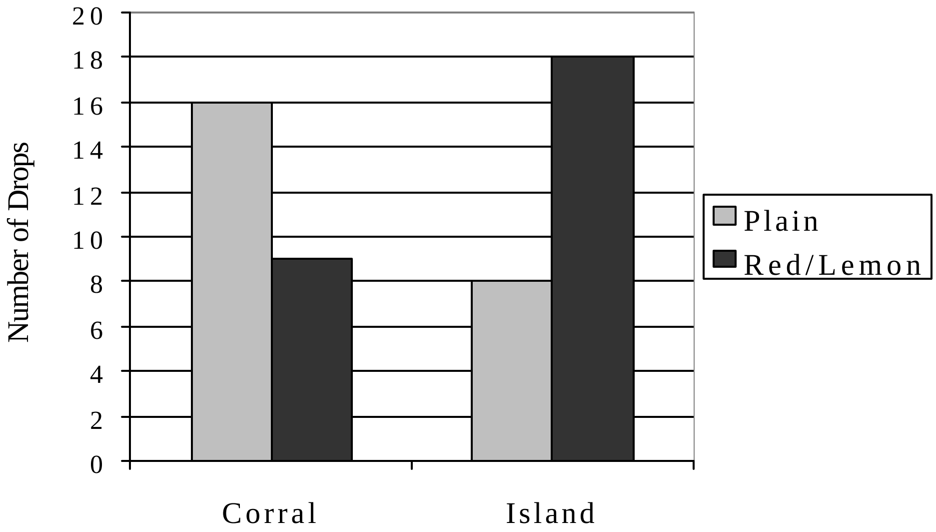

Figure 2. Number of drops observed in corral-housed rhesus macaques.

(χ^2(1, N = 60) = 4.44, p < .05) and novel chow less often (χ^2(1, N = 60) = 5.45, p = < .05) than island monkeys dropped these foods.

Ten of the males in experiment two received both types of test food. Analyses on these repeated measures found no differences in manipulation time, frequency of sniffs, or number of drops observed for novel and familiar food.

Methods for Experiment Three: Food Source

Subjects

Fifty-seven males and fifty-nine females (N = 116) from the island colony served as subjects in one of four conditions: (a) familiar food delivered by the experimenter (n = 30), (b) novel food delivered by the experimenter (n = 30), (c) familiar food encountered by the subject (n = 28), or (d) novel food encountered by the subject (n = 28).

Procedure

In the delivered condition the experimenter hand-tossed test food to subjects. In the encountered condition food was placed in the monkey's habitat before sunrise. Encountered food pieces were placed along trails and within the vicinity of feeding sites where animals first traveled each day. To insure that subjects were encountering pieces for the first time, a small number of food pieces was used per day, so that they could be accounted for, and each social group encountered novel foods only once. The experimenter wore gloves when handling food to preclude olfactory cues pertaining to the source of the food. Foods were peeled and cut into similar small pieces (approximately 1 x 2 x 3 cm). Three different foods were used in each condition. Novel foods for this experiment included kiwi, mango, and unsalted rice cake. Familiar foods included apple, banana, and monkey chow. Foods in each category were only compared to each other (familiar delivered vs. familiar encountered, novel delivered vs. novel encountered) so palatability and nutrient content were not confounding factors in this experiment.

It was expected that animals would have longer manipulation times, a higher frequency of sniffs, and a higher rate of dropping novel foods in the encountered versus delivered condition. No such differences were expected for familiar food.

Results for Experiment Three

Subjects dropped novel foods significantly more often when food was encountered (17 drops out of 28 trials, 60.7%) as opposed to delivered (8 drops out of 30 events, 26.6%), (χ^2 (1, N = 58) = 6.63, $\underline{p} < .001$, Figure 3). There was no difference in the rate of drops for familiar food between the two conditions. There were no differences in manipulation time or number of sniffs directed toward novel food between the encountered and delivered conditions.

Three post-hoc tests were run on the data from the novel delivered versus the familiar delivered conditions to test for neophobia. The monkeys handled novel food longer ($\underline{t}(58) = 2.45$, $\underline{p} = .017$) and sniffed it more often ($\underline{t}(58) = 3.64$, $\underline{p} = .001$) than familiar food. There was no difference in the number of drops for novel versus familiar food unless kiwi, the sweetest of the three novel foods, was left out of the analysis (χ^2(1, N = 20) = 4.36, $\underline{p} < .05$).

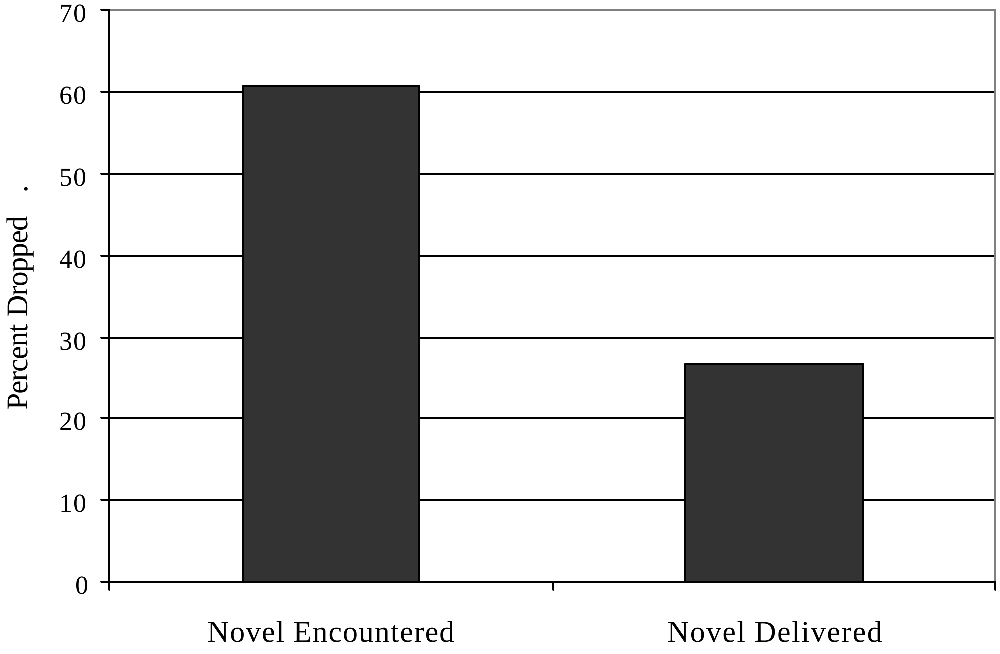

Figure 3. Percentage of trials that ended with a drop for novel encountered (n = 28) and novel delivered (n = 30) test food.

Methods for Experiment Four: Age Effects

Subjects

Forty 1-year olds, forty 2-year olds, and forty monkeys 5 years or older (adults) from the island colony served as subjects. Equal numbers of males and females were tested in each age group.

Procedure

Half the data were collected from mid-May thru mid-June (the end of the birth season) and the other half from mid-October thru mid-November (breeding season). The availability of naturally occurring food may have differed between these two data collection periods so time of year was controlled for by observing equal numbers of subjects in each age and food category in the spring and fall. Note, however, that the 1-year old and 2-year old age categories include animals that are 1.5 and 2.5 years old.

Because older and more dominant individuals prevent the youngest animals from encountering test food pieces, it was necessary to distract other group members during trials. Therefore, the experimenter broadcast corn, a familiar food, by the handful to groups of monkeys. Once group members were foraging on the broadcast food, the experimenter continued to toss out individual food pieces. Some of these pieces were novel and were directed toward particular animals that served as subjects. Familiar food for this experiment was monkey chow. Novel foods included green pepper, yellow squash, parsnip, cheese- flavored crackers, canned white potatoes, canned Italian cut green beans, oyster crackers, cucumber, shredded wheat cereal, and breadsticks. To insure that these test foods were palatable, trials were conducted with male macaques that had been trapped and were singly housed on the island (Appendix A).

In addition to recording food-directed behavior, as described in experiment one, the subjects' sex, ID number, and age group were noted. Subjects' ages were confirmed by cross checking their ID with their birth date in the colony records. The original research design included a 3 to 4-year old age category. However, too few males could be located to serve as subjects primarily due to heavy culling of this cohort in recent years. If food neophobia is a learned behavior it was expected that 1-year olds would not be neophobic, that adults would be neophobic, and that 2-year olds might show some intermediate level of food neophobia. Neophobia was measured as longer manipulation times, higher frequency of sniffs, and a higher frequency of drops for novel compared to familiar food.

Results for Experiment Four

An ANOVA found a main effect of age on manipulation time ($\underline{F}$ (2, 108) = 0.699, $\underline{p}$ = .000, Figure 4) but no effects of sex or food type. Tukey's HSD post-hoc test indicates that one-year olds handled food longer than adults ($\underline{M}_{\text{1-year old}}$ = 92, $\underline{M}_{\text{2-year old}}$ = 55.4, $\underline{M}_{\text{adult}}$ = 31.8 seconds). There were no significant differences between the manipulation times observed in 1-year olds versus 2-year olds or 2-year olds versus adults.

Planned comparisons (t-tests) were conducted on the data for individual age groups. There were no significant differences between the manipulation times for novel versus familiar food within the one-year old and adult age categories. It was hypothesized that one-year old animals would not be neophobic, therefore it is notable that their sample means for manipulation time were in the opposite direction expected if they were neophobic ($\underline{M}_{\text{familiar}}$ = 104.3, $\underline{M}_{\text{novel}}$ = 79.8 seconds). The mean manipulation time for the

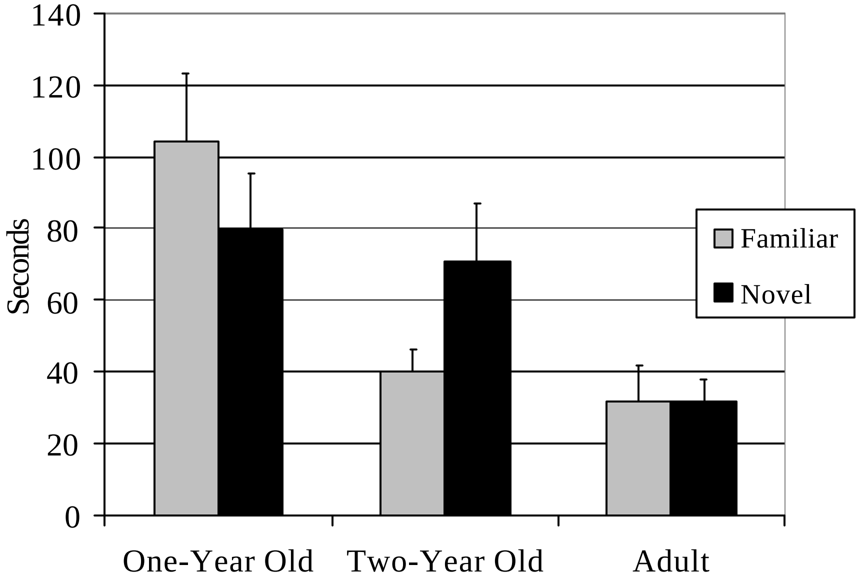

Figure 4. Mean manipulation time (+SE) for familiar and novel foods within each age group.

two-year olds was greater for novel food ($\underline{M}_{familiar}$ = 40, $\underline{M}_{novel}$ = 70.8 seconds; $\underline{t}(38)$ = 1.77, $\underline{p}$ = .042, one tailed) as expected for neophobia.

Data collected in the spring were compared to those collected in the fall within each age group primarily to test whether 1.5 year olds differed from 1-year olds. In all age groups, the sample means for manipulation time of both food types was lower in the fall, but not significantly lower.

Again post hoc tests were run to see if subjects that served in multiple experiments biased the data. Data from eight (five males and three females) of the 40 adult subjects were eliminated from the analysis to test whether serving in multiple experiments caused animals to decrease their manipulation time for novel foods. If this was the case then the mean manipulation time for the remaining subjects would increase creating a bigger difference between the sample means for familiar and novel foods. However, the mean manipulation time of novel foods for the 14 experimentally naive animals was lower, though not significantly lower ($\underline{M}$ = 26 seconds), than that calculated when including data from the 8 experienced adults ($\underline{M}$ = 31.7 seconds). So the eight experienced animals did not bias the data in the direction expected.

For frequency of sniffs there was a significant interaction between age and sex. While males directed fewer sniffs toward food with increasing age ($\underline{M}_{1\text{-year}}$ = 4.2, $\underline{M}_{2\text{-year}}$ = 2.7, $\underline{M}_{adult}$ = 2.6 sniffs) females' frequency of sniffs increased with age ($\underline{M}_{1\text{-year}}$ = 3.1, $\underline{M}_{2\text{-year}}$ = 3, $\underline{M}_{adult}$ = 5.5 sniffs).

Chi-square tests found no relationship between subjects’ age or sex and the likelihood of dropping the test food. Novel foods were dropped more often than familiar foods in all three age groups (χ^2 (1, $\underline{N}$ = 120) = 26.25, $\underline{p}$ < .001, Figure 5). Of the 60 trials

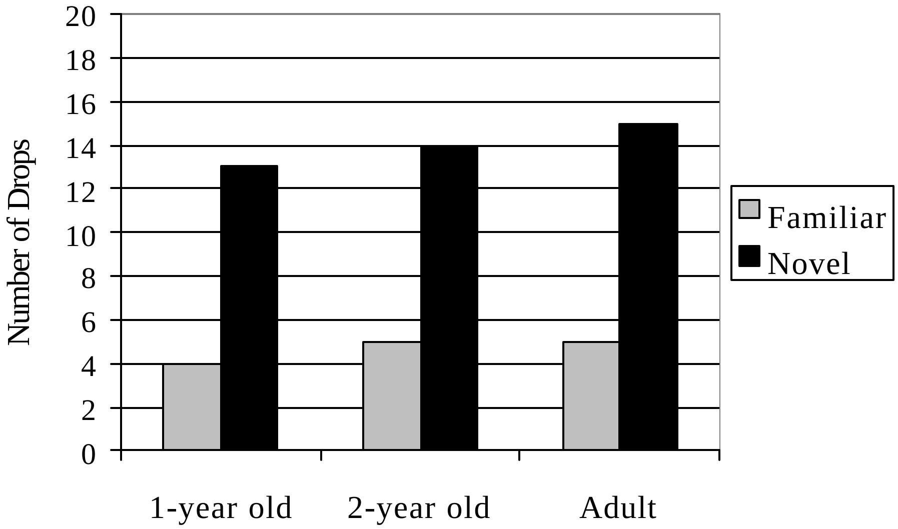

Figure 5. Number of drops observed for each food and age group.

conducted for each food type, familiar foods were dropped on 14 trials and novel foods were dropped on 42 trials. There was no interaction between age and food type on the likelihood of drops.

Methods for Experiment Five: Sugar Content

Subjects

The subjects were 18 male rhesus macaques aged five years or older. Only nine subjects provided suitable data for analysis. Of the nine subjects that did not complete the study, one subject was mistakenly given both the sugar containing test foods on trial one, four animals stopped taking food altogether (including their daily chow in two cases), and three animals would not take test food while the experimenter was present. These males were available for study while being held in single cages on Morgan Island. The males were taken from the free-ranging population five to eight days prior to the start of data collection and were available for four days of observation before being transported to another facility.

Procedure

Two pairs of test foods were used. One test food pair was made using a basic cookie recipe (flour, milk, butter, rolled oats, eggs, salt, red food coloring, and sugar or no sugar) and will be referred to as sugar and no-sugar biscuits. The sugar biscuits contained 31% sugar, measured by dry weight, and the no-sugar biscuits contained 0% sugar. The second pair of foods was commercially available bread sticks and cookie sticks that looked very similar but contained different amounts of sugar (6.6% vs. 32% of dry weight per serving).

On trial one, subjects were sequentially given one food from each pair. Half the subjects received the sugar biscuit and the breadstick and the other half received the no-sugar biscuit and the cookie. On trials 2 through 11 all subjects received the no-sugar test food from each pair. Multiple exposures to the non-sugar test food were intended to make this food familiar to the subjects. The subjects' behavior was recorded, as described in experiment one, on trials 1, 2, and 11.

If macaques do not exhibit food neophobia toward foods containing sugar then a number of predictions should hold. First, subjects that have sugar food on trial one should treat it as familiar and show no differences in manipulation time, frequency of sniffs, and the rate of drops between trial 1 and trial 11, when they get a similar but non-sugar food that has become familiar. Subjects should, however, exhibit a neophobic response to a no-sugar food, showing longer manipulation times, more sniffs, and more drops on trial 1 compared to trial 11 when this same food is familiar. A third hypothesis is that subjects will show shorter manipulation times, a lower frequency of sniffs, and a lower likelihood of dropping sugar-containing food on trial one compared to trial two with the similar but no-sugar food because the sugar food, though novel, will not elicit neophobia while the novel no-sugar food will.

Results Experiment Five

Subjects sniffed the no-sugar foods less often on trial 11 compared to trial 2 indicating that the no-sugar food was treated as familiar after ten presentations (F (1,21) = 12.12, p = .002). When a sugar-containing novel food was presented on trial 1, there were no differences in manipulation time, frequency of sniffs, or frequency of drops for trial 1 compared to the now familiar no-sugar food on trial 11. However, when a novel no-sugar food was presented on trial 1, subjects sniffed the food more often on trial 1 compared to trial 11 when this same food was familiar ($t(8) = 5.21$, $p = .000$, one tailed). There were no differences in manipulation time or the frequency of drops for the no-sugar foods between trial 1 and trial 11. The third hypothesis was supported as subjects handled a novel sugar food for less time ($t(8) = 1.94$, $p = .04$, one tailed) sniffed it less often ($t(8) = 1.92$, $p = .04$, one tailed) and dropped it less often ($\chi^2(1, 18) = 5.55$, $p < .05$) on trial one compared to trial two which was their first exposure to the no-sugar version of the test food.

Meta-analysis of Hypotheses Tested

During the analyses for all five experiments, there were 21 comparisons where a neophobic response was expected. Although few of the comparisons were statistically significant, in 18 of them, the difference between the sample means was in the direction predicted (Table 1). This is significantly more common than expected if there had been no effect of novel food on the macaques' behavior (binomial test, $p<.000$).

Table 1

Were the sample mean differences in the direction expected for food neophobia?

Comparison	Manipulation Time	Frequency of Sniffs	Number of Drops
Experiment One novel vs. familiar food in island macaques	yes	yes	yes
Experiment Three novel delivered vs. novel encountered food	yes	yes	yes
Experiment Four			
Two-year olds: novel vs. familiar food	yes	yes	yes
Adults: novel vs. familiar food	no	yes	yes
Experiment Five			
no-sugar trial 1 vs. no-sugar trial 11	no	yes	no
sugar trial 1 vs. no-sugar trial 2	yes	yes	yes
no-sugar trial 2 vs. no-sugar trial 11	yes	yes	yes

Note: Experiment Two (corral-living macaques), one-year olds in Experiment Four, and the comparison of sugar on trial 1 vs. no-sugar on trial 11 from Experiment Five, were not included as neophobia was not predicted in those cases.

CHAPTER 3: DISCUSSION

The aim of this dissertation was to study aspects of food neophobia in a generalist species. Predictions about the behavior of rhesus macaques toward novel foods were derived from the hypothesis that food neophobia is learned and based on a history of conditioned taste aversions with novel foods. Results from four of the five experiments were consistent with this hypothesis. More data are needed on younger animals to understand how neophobia changes with age.

Experiments one and two revealed a marked contrast between the food-directed behavior of non-human primates living in a restrictive captive environment versus more natural conditions. The neophobic response (as indicated by the number of drops) of island-living rhesus macaques increased with increasing novelty of the test food while corral-housed macaques did not exhibit neophobia. It appears that the corral animals not only lack food neophobia but may even prefer novel food, as this sample of monkeys ate novel chow more often than plain chow. This result is similar to results reported by Fragaszy, Visalberghi, & Galloway (1997) who found that infant capuchins preferred novel to familiar foods. The data reported here show that food neophobia is not evident in traditionally-housed captive primates. Studies on food-related behavior in captive primates should be interpreted cautiously with respect to their generalizability to unprovisioned, wild populations.

That corral-living females sniffed food less often then males was unexpected. Perhaps because females are more often than males in close proximity to other animals (Bernstein & Draper, 1964) they were more often interrupted by curious on-lookers.

However, if this was the case, then a sex difference in manipulation time would also be expected, but it was not found. Therefore, possible sex differences in the probability of interruption cannot be a complete explanation for the sex difference observed in the number of sniffs.

Independent palatability trials were not conducted for the novel foods used in experiments one and two. However, corral-housed animals ingested the red/lemon novel food at a high rate, indicating that this food is indeed palatable to rhesus macaques. As for the red chow and lemon chow in experiment one, it should be noted that more subjects ate, rather than dropped, these foods (19 eats out of 30 trials for red and 20 eats out of 30 trials for lemon). Therefore it can be concluded that these foods are palatable to rhesus macaques. If, however, the red chow and lemon chow, though palatable, are not as preferred as plain chow, then the results of experiment one might reflect preferences rather than neophobia. Control data are needed before the results of experiment one can be properly interpreted.

The hypothesis that humans serve as a learned safety signal was supported by the fact that island-living macaques were more likely to eat a novel food if it was hand-tossed to them by the experimenter rather than encountered in their environment. The method of delivery did not affect whether familiar food was eaten or dropped. This conclusion partly explains the lack of neophobia observed in the corral-housed animals. All of their food is provided by humans, so they grow up learning that humans are a source of safe, nutritious food.

The hypothesis that young animals are not neophobic was not supported. If 1-year old monkeys were not neophobic they would drop and eat novel and familiar foods at equal rates. However, novel foods were dropped more often than familiar food in all three age groups. Based on these data it must be concluded that macaques as young as 1-year old do exhibit food neophobia.

Social facilitation may have influenced the behavior observed in experiment four. To get test food to young animals, familiar food was broadcast to groups of monkeys. Animals feeding surrounded the subjects. However, social facilitation should encourage food acceptance, and young animals dropped novel foods at a rate similar to the other age groups.

Before ruling out the possibility that food neophobia is learned, data should be collected with younger animals. At the end of the fall data collection period the author attempted to conduct trials with 5 to 6-month old infants. Handfuls of a familiar (corn) or novel (green pepper, potato) food were broadcast to groups of animals with infants present. The most striking observation was the availability of social cues that could influence infants' feeding behavior. When corn was thrown, all animals quickly gathered and ate food pieces. When novel food was thrown there was much less activity as adults and juveniles sat, looked, and only occasionally picked up and sniffed food pieces. Systematic observations of infants in these testing conditions would reveal the presence or absence of food neophobia in this age group and the extent to which infants' behavior depends on the feeding behavior of their group members. If infants do exhibit neophobia when they begin to forage independently, then the CTA hypothesis must be discarded.

Adults in experiments one and four manipulated novel and familiar food equally. This result was unexpected as adults in a previous study on this population reliably manipulated novel foods longer (Johnson, 2000). For example, in the previous study, when comparing macaques' manipulation time for chow (M = 19.4 seconds) versus canned beets, a novel but palatable food, (M = 62 seconds) sample sizes of 30 per group resulted in an effect size of d = .99 (Johnson, 2000). The effect size (d) is a measure of the difference between the sample means divided by the variation within the groups, and it reflects the magnitude of the effect the treatment has on the dependent variable. An effect size of .99 is large, meaning differences could be found using fewer subjects (Cohen, 1988). However, data from the adult subjects in experiment four of the current project came from 20 animals per cell and the effect size was only d = .005, even though the pooled standard deviation of the current subjects (S = 36.8) was less than that for the previous study (S = 42.9). This suggests that the non-significant findings of the present experiment are valid and not due to a lack of power.

It is possible that the adults did not manipulate novel food longer because the experimenter came to serve as a learned safety signal during the course of the experiments. The author studied this population in 1996 and early 1997 so the adults were familiar with her but the current one-year and two-year olds were not. In experiment four, however, analysis of data collected in the spring versus that collected in the fall revealed no significant differences. The explanation that adult subjects serving in multiple experiments biased the data was also not fully supported. According to post hoc tests, subjects who served in multiple experiments may have sniffed food less often, thus obscuring a possible difference between groups, but they did not alter the mean manipulation times in a way that would explain the results. Food neophobia is still inferred in both experiments from the fact that adult subjects were more likely to drop novel compared to familiar food.

Finally, food neophobia was not elicited when the novel food contained a high percentage of sugar. Macaques sniffed a no-sugar novel food on trial 1 more then on trial 11 but when the novel food contained sugar there was no difference between trial 1 and trial 11. No-sugar foods on trial two were handled longer, sniffed more, and dropped more often compared to the similar but sugar-containing food on trial one. This result is especially notable because, although trial two was subjects' first exposure to the no-sugar food, it was similar to trial one in every way except sugar content. The size, appearance, texture, and method of delivery were identical to trial one. Under these conditions the test food was in many ways familiar, yet subjects treated the trial two food more cautiously then the sugar-containing trial one food.

That monkeys will readily accept a sugar-containing novel food is not surprising. Preference for sweet foods is currently considered innate in humans. Steiner & Glaser (1984) tested human neonates with a .4 M sucrose solution before their first contact with tastants or food. They observed a gustofacial reflex typical of acceptance and liking. The reactions of an adult male, adult female, and juvenile male rhesus macaque (Macaca mulatta) to the same solution matched that of the human neonates and 11 other non-human primate species (Steiner & Glaser, 1984). Though no infants were tested in this study, one might conclude that macaques, like humans, are born with a preference for sugary tastants. Therefore, if a primate did learn to be neophobic and approach novel foods cautiously, the detection of sugar might mask or inhibit neophobia because the animal likes sugar, not because it learned an association between the taste of sugar and positive post-ingestive effects.

The first study comparing novel and familiar foods in this population (Johnson, 2000) found significant differences in all three dependent variables. This was rarely the case in the experiments reported here. As discussed previously, the alpha level adopted for these experiments could have been adjusted to account for multiple measures used to test for neophobia. The only notable change incurred by adopting this stricter level ($p < .017$) would be that island monkeys did not significantly drop red/lemon chow more than plain chow in experiment one. Retaining the more liberal rejection criteria ($p < .05$) is supported by a meta-analysis of the major hypothesis tested.

In conclusion, the current experiments demonstrate that housing conditions and whether or not food is hand-tossed by a human observer affect the expression of food neophobia in rhesus macaques. These results support the hypothesis that food neophobia may develop from a history of CTA. However food neophobia is already apparent in rhesus macaques as young as 1-year old. Further experiments must be conducted with younger animals to confirm an ontogenetic shift in the direction or magnitude of preferences for familiar and novel foods predicted by the CTA hypothesis.

These results provide a starting point for investigating the role of food neophobia in non-human primate feeding ecology. Additional studies on individual differences, the development of the behavior, and species differences should further understanding of the behavior and its ultimate role in species survival in changing habitats. For example, individuals clearly vary in their behavior toward novel food. Although novel foods were reliably dropped more often than familiar foods in most of these experiments, there were certainly animals that ate novel foods. Wilson, Clark, Coleman, & Dearstyne (1994) discussed the connection between neophobia and the traits of shyness or boldness in individuals. The rank of individual subjects in the dominance hierarchy of a rhesus macaque group might affect whether or not they approach novel food and how long they investigated food before eating or dropping it. Also, if Rozin & Kalat (1971) were correct in suggesting that generalist feeders are specially adapted to learn to avoid certain foods, then food neophobia might be found to co-vary with the feeding ecology of different primate species.

Regarding the application of these findings to conservation it should be noted that even young animals may be neophobic if translocated to an area with new food sources. In this case any measure taken to help prepare a group for translocation, such as providing experience with the foods they will encounter, should incorporate all group members including the youngest.

Food neophobia is obviously a component of the feeding strategy of primates. Although it may not be observed in traditionally-housed captive primates it can be readily seen in free-ranging, though provisioned, groups. Therefore neophobia must be incorporated into any comprehensive explanation of the feeding ecology of primates.

APPENDIX A: PALATABILITY TRIALS

	Trial 1	Trial 4	Trial 7	Trial 10
green pepper	2/4	3/4	4/4	---
yellow squash	2/4	3/4	3/4	---
parsnip	2/4	3/4	3/4	---
cheese flavored cracker	1/3	3/4	3/4	---
dog treat*	0/3	1/5	1/4	---
mushroom w/ maple odor*	0/4	0/4	0/4	---
canned white potato	6/9	7/9	4/9	5/9
canned green bean	2/8	5/8	7/8	6/8
oyster soup cracker	8/10	9/10	7/10	7/10
cucumber	6/9	9/9	8/9	7/9
shredded wheat cereal	9/10	9/10	10/10	10/10

Note. Ratio is the number of animals that ate a piece of test food put in their cage to the total numbered offered the food. Dashes (---) indicate testing stopped at trial 7.
* These foods were judged unpalatable and not used in experiments.

APPENDIX B: REVIEW OF THE LITERATURE

Neophobia is defined as a fear of novelty. Neophobia towards food has been studied in a number of species. It is usually recognized and measured by an animal's tendency to eat less of a novel food compared to a familiar food on the first presentation. However, more conspicuous behaviors associated with neophobia can be observed. Many species exhibit a longer latency to even taste a novel food compared to a familiar food (Barnett, 1958; Mitchell, 1976). Domestic sheep will completely refrain from eating a novel food, or even a familiar food in a novel container, for three to five days (Chapple & Wodzicka-Tomaszewska, 1987). Coppinger described the reaction of blue jays to novel butterfly prey as a sequence of behaviors including alarm calls, retreat from the food source, crest raising, and frantic flying about the cage while banging into the walls (cited in Domjan, 1977).

The role of neophobia is important when asking questions about how an animal responds to changes in food resources, how specific diets are acquired, how an animal decides which foods to add to its diet, and the likelihood that a species will exploit new resources and niches when given the opportunity. Just as optimal foraging theory allows us to identify the constraints and currencies that are important to animal foraging behavior, so too will the study of food neophobia allow us to generate and test hypotheses that will lead to a greater understanding of how animal diets develop, specific food choices, and a species' ability to respond to changing resources and environments.

Neophobia is most often discussed in relation to feeding. Domjan (1977) reviewed the topic of neophobia for edible substances and provides a history of how the behavior was first recognized in "bait shy" rats (also see Rozin, 1976). Table 1 lists citations from Domjan (1977) that illustrate the range of species in which neophobia has been described. The bulk of the data on neophobia comes from work with the genus Rattus, shown here by the numerous references cited for rats.

Table 1. Citations from Domjan (1977)

Birds	chicken	Capretta, 1969 Capretta & Bronstein, 1967
	blue jay	Coppinger, 1969; 1970
	wild birds	Morell & Turner, 1970
	zebra finch	Rabinowitch, 1968; 1969
Dogs		Maslow, 1932
Fish	Atlantic cod	Mackay, 1974
	sunfish	Miller, 1963
Guinea Pigs		Warren & Pfaffmann, 1959
Humans		Hollinger & Roberts, 1929 Rozin, 1976
Rats		Barnett, 1956 Barnett & Spencer, 1953 Capretta & Rawls, 1974 Domjan & Bowman, 1974 Gentile, 1970 Green & Parker, 1075 Nachman & Jones, 1974 Navarick & Strouthes, 1969 Sheffield & Roby, 1950 Siegel, 1974 Singh, 1974 Shortens, 1954 Young, 1944
Turtles	snapping turtle	Burghardt & Hess, 1966

Table 2 lists citations related to neophobia in feeding since 1977, as well as four notable studies not included in Domjan's review (Barnett, 1958; Mitchell, 1976; Rodgers

Table 2. Citations for Neophobia In Feeding Since 1977

Birds	mockingbird	Barrows et al, 1980
	chicken	Jones, 1986
	jackdaw	Katzir, 1983
Cats		Bradshaw, 1986
Cockroaches		Geissler & Rollo, 1987
Fish		Morgan & Colgan, 1988
		Wilson et al, 1994
Gerbils/ Hamsters		Forkman, 1991
		Wong & McBride, 1993
Primates	rhesus macaque	Johnson, 1998
		Weizkrantz & Cowey, 1963
	tufted capuchin	Fragaszy, Visalberghi, & Galloway, 1997
		Visalberghi & Fragaszy, 1995
	common marmoset	Vitale & Queyras, 1997
	mantled howler monkey	Whitehead, 1986
Rats		Barnett, 1958
		Brunton, 1995
		Cowan, 1977
		Daly et al, 1982
		Feild, Kasper, & Mitchell, 1984
		Galef, 1993
		Kronenberger & Medioni, 1985
		McFayden-Ketchum & Porter, 1989
		Mitchell, 1976
		Rodgers & Rozin, 1966
Ruminants/Sheep		Buritt & Provenza, 1991
		Chapple & Lynch, 1986
		Chapple & Wodzicka-Tomaszewska, 1987; 1987
		Provenza & Balph, 1988

& Rozin, 1966; Weizcrantz & Cowey, 1963). I will comment on a few papers that highlight different aspects of animals' neophobic responses to food.

Neophobia in most species eventually disappears with repeated exposure to a new, palatable food. For example, cats offered a familiar or novel flavored food, preferred the familiar food on the first day of presentation (Bradshaw, 1986). On the second presentation they increased their consumption of the novel food. However, after 102 days of no exposure, the cats' original level of neophobia returned. Also, exposure to only the odor of the food was not enough to attenuate their initial intake of the novel food (Bradshaw,1986).

Jones (1986) observed the neophobic responses of two strains of domestic chicks and found that neophobia can be modified by several factors. The 'S' strain chicks fed sooner, longer, ate more, and jumped (a fearful response) less during the observation period while eating a novel food (blue colored mash) then did the genetically different 'T" strain chicks (Jones, 1986). Jones then gave one group of chicks a different colored mash each day for three days (green, yellow, and red) while a control group received uncolored mash. Both groups received blue mash on day four. The group that had experience with colored mash fed sooner, longer, and displayed less jumping and preening during the feeding period (Jones, 1986). A final group of chicks was housed for two weeks in an enriched cage; one that had various novel objects placed in it at regular intervals. When tested with novel food, chicks in these enriched environments spent more time feeding and jumped less during feeding than chicks from non-enriched environments (Jones, 1986). A sex difference in chicks' neophobic response was also observed in that females fed sooner, longer, ate more, and closed their eyes (a fearful response) less then males under similar conditions (Jones, 1986). These data demonstrate that neophobic responses in domestic chicks can be affected by genetics, sex, experience with novel foods, and a varied environment.

Cockroaches share a distinction with humans and rats as being true omnivores (Rozin, 1976). As such, it can be expected that neophobia plays a role in diet selection for cockroaches as it does for rats. Geissler & Rollo (1987) disrupted the neophobic response of cockroaches by varying their subjects' nutritive intake. One group ate a well-balanced diet for three weeks while the experimental group ate a non-nutritive diet for six weeks. Both groups were then offered their familiar diet and a novel nutritive diet. The well-nourished group preferred to eat their familiar food and only sampled the novel food. Malnourished subjects did not retain this preference for familiar food but spent 70% of their time sampling the novel food (Geissler & Rollo, 1987). So nutritional status appears to affect neophobic responses. However, it must be noted that the results obtained by Geissler & Rollo (1987) may be the result of a learned aversion to a non-nutritive food (Rozin, 1976). However, Johnson (2000) found that a group of provisioned rhesus macaques living in a natural environment continued to exhibit taste neophobia even when provisioning was temporarily blocked. So it is possible for species to experience some change in nutritional status with no effect on their neophobic response.

Neophobia in Social Learning

Researchers studying social learning have a particular interest in food neophobia. The ability to gain information about a new food source from others would lessen the risk to an individual who might otherwise be exposed to a harmful substance.

For many years Bennett Galef focused his research program on the mechanisms of diet choice in rats. He demonstrated that information from conspecifics (odor cues from another rat’s breath) influences food preferences in Norway rats (Rattus norvegicus) and that this method of social learning is particularly salient for novel foods (Galef, 1993; 1996).

Visalberghi and Fragaszy (1995) investigated the effect of social context on neophobia in captive tufted capuchin monkeys (Cebus apella). The capuchins always ate more familiar then novel food regardless of social context yet 9 of 11 individuals ate more types and greater amounts of novel food in the social versus individual testing condition (Visalberghi & Fragaszy, 1995). These results agree with Galef’s work that suggests social facilitation has a greater effect on the intake of novel compared to familiar foods. Similar results were also reported by Forkman (1991) who found social facilitation acted on gerbils’ response to novel but not familiar food.

Vitale & Queyras (1997) looked at social facilitation in common marmosets (Callithrix jacchus). Again, social context had an effect on young marmosets intake of novel but not familiar foods (Vitale & Queyras, 1997). Young marmosets were more likely to keep eating a novel food when they had visual or physical access to the rest of their group then when they were only paired with another food-naive young individual (Vitale & Queyras, 1997). Notably, these young marmosets did not show any difference in the number of times they fed on familiar and novel foods during baseline conditions (Vitale & Queyras, 1997).

Katzir (1983) carried out a unique investigation into the role of social rank on neophobia. He hypothesizes that lower ranking individuals should be more likely to exploit new feeding resources as a means of keeping ahead of the competition from other group members. Though small sample sizes kept his results from reaching significance, he did find that in the six groups of captive jackdaws he tested, the “initiator” (birds that fed sooner and longer on a novel food) in four groups was the lowest ranking bird and in two groups was a mid-ranking bird. In no group did the highest ranking bird act as an initiator (Katzir, 1983). The relationship between social rank and propensity to exploit new resources could be an indirect result of an individual’s state of hunger that results from differential access to a food source. However it appears to be a useful avenue to explore and will hopefully be the focus of additional studies.

Neurophysiology of Neophobia

There is a distinct literature on the physiological basis of generalized neophobic behavior (e.g. Britton, Ksir, Thatcher-Britton, Young, & Koob, 1984; Cole, Robbins, & Everitt, 1988; Mason, Roberts, & Fibiger, 1978; Pisa, Martin-Iversen, & Fibiger, 1988; Rolls & Rolls, 1973). These studies demonstrate the importance of adrenergic receptors in the forebrain as mediators of the neophobic response to food. For example, lesions in rats' dorsal noradrenergic bundle deplete norepinephrine (NE) in the forebrain and are reported to either enhance or attenuate food neophobia depending on the behavioral testing conditions (Steketee, Silverman, & Swann, 1992). Subsequent infusion of NE into the lateral ventricles of lesioned animals reverses this shift in food preference (Steketee, Silverman, & Swann, 1992). One of the most interesting papers found that neophobia, but not learned taste aversion, was attenuated by any of three different lesions to the ascending olfactory pathways (Royet & Pager, 1982). Therefore, physiologically speaking, these two traits are indeed separate and neophobia in rats depends on a fully intact olfactory pathway (Royet & Pager, 1982).

The Neophobia Model

Rozin (1976) describes the feeding strategies of generalists (or omnivores) as versatile and flexible in food choice. This approach gives species a great advantage in that they are able to adapt to a changing environment, unlike strict dietary specialists that may perish if their food source is compromised. The catch, however, is that experimentation can be dangerous, as many substances are harmful if ingested. For these reasons, omnivores, such as rats, cockroaches and humans, may display both exploratory tendencies as well as an avoidance of new things (Rozin, 1976). Rats typically solve this approach-avoidance conflict by ingesting small amounts of a new food then avoid the food for a time during which taste-aversion learning (also called conditioned taste aversion, CTA) can occur if the food is harmful. This pattern of poison testing is observed as a neophobic response but allows the generalist to test potential food sources with minimal risk. In fact, Rozin and Kalat (1971) suggest that CTA is an adaptive specialization of generalist feeders and thus may not be as readily observed in a species that are specialized feeders.

To test Rozin & Kalat's (1971) hypothesis concerning the relationship between a species’ feeding ecology and conditioned taste aversion learning, Daly, Rauschenberger, & Behrends (1982) looked at two kangaroo rat species’ ability to learn conditioned taste aversions. One species (Dipodomys merriami) was categorized as a generalist while the other (Dipodomys microps) was considered a dietary specialist. Though both species learned aversions to novel foods, the generalist species learned sooner (after one trial instead of two) and was able to learn aversions to both foods used while the specialist seemed to prefer one of the test foods regardless of its induced illness (Daly et al, 1982). However, while expecting generalists to learn taste aversions more quickly than specialists, it should also be expected that generalist species are less neophobic than specialists (Greenberg, 1983). The behavior of the kangaroo rats does not fit this prediction, however as *D. microps* appeared to be less neophobic than *D. merriami* (Daly et al, 1982). In the first hour that three novel foods were simultaneously presented, 10 of 13 *D. microps* sampled at least one food but only 6 of 13 *D. merriami* did so. After 23 hours of exposure, all of 13 *D. microps* had sampled three novel foods presented to them while 6 of 10 *D. merriami* had only sampled two. The authors were interested in the pattern of sampling. Because *D. merriami* separated sampling the new foods they argue it comes closer to a pattern expected if the animals were poison testing. Allowing time to elapse between sampling would support conditioned taste aversion learning. Also, future observations revealed that although *D. microps* from this study site fed almost exclusively on chenopod plants (*Atriplex confertifoloa*) and have a special chisel tooth which allows them to exploit these plants, in other locations this species' diet contains a larger variety of items so it may be incorrect to classify it as a strict dietary specialist (M. Daly, person. comm.).

In conclusion, neophobia is posited to function as an adaptive strategy that protects individuals from ingesting toxins or poisons from unknown food sources (Rozin, 1976; Visalberghi, 1994). The evidence for neophobia's function and the role of conditioned taste aversion in this process of avoiding novel foods is strong for rats (Galef, 1993; Richter, 1953; Rozin, 1976; Rozin & Kalat, 1971) and should be studied in other species with particular attention paid to the subject's feeding ecology.

Greenberg’s “Neophobia Hypothesis”

An exciting aspect of neophobia is the possibility that this behavioral trait impacts a species' ability to survive beyond placing constraints on feeding. Russell Greenberg (1990) notes that species differ in their tendency to exploit a new resource and that this is due to a difference in ecological plasticity. Ecological plasticity refers to the breadth of environments, niches, or resources that a species is able to use. If one could measure ecological plasticity, it might be possible to explain why some species give rise to adaptive radiations while others do not.

Ecological plasticity is difficult to measure. However, Greenberg (1990) proposed that neophobia in fact determines plasticity and thus is a good measure of the trait across species. A highly neophobic species will be less likely to explore and exploit new niches or food sources, while less neophobic species will do so more readily. It is the less neophobic species that are more likely then to expand their niche when given the opportunity.

It can be expected that degree of neophobia will correlate highly with a species’ feeding ecology. Generalists feeders should show low levels of neophobia relative to specialist feeders which are closely related morphologically and live in the same environment. Greenberg (1983) found precisely this relationship when looking at the neophobic response of two morphologically similar warbler species that live sympatrically. Both Bay-breasted and Chestnut-sided warblers are foliage gleeners, yet Bay-breasted warblers forage in a greater range of heights, and on a greater diversity of plants and surfaces (Greenberg, 1983). In a series of feeding experiments using novel objects as feeding containers, Greenberg (1983) found that though the two species did not differ in the number of approaches to the objects, the Bay-breasted warblers (the generalists) were more likely to feed after approaching and a greater percentage of the Chestnut-sided warblers approaches were “far approaches”. There was also a difference in each species’ latency to approach the feeding site, in that the Bay-breasted warblers approached objects sooner. These results support the hypothesis that there is a relationship between a species’ feeding ecology and degree of neophobia. This could be extended to predict that if neophobia determines a species' ecological plasticity, feeding ecology will correlate with a species' ecological plasticity and the likelihood of niche expansion.

Neophobia could also be considered from the same perspective as the shyness-boldness continuum that has been studied in humans and some animal species. This behavioral trait varies between individuals and may also vary systematically between species (Wilson, Clark, Coleman, & Dearstyne, 1994). The relationship between the two concepts is direct in that "boldness" can be defined as either risk taking or the propensity to approach novel situations (though these are assumed to be separate behavioral traits)(Greenberg, 1995). Wilson et al (1994) call for more comparative work to be done on this topic so that the adaptive aspects of shyness and boldness might be considered for all taxa. Greenberg (1995) considers neophobia a behavior that can simultaneously be considered from a psychological and behavioral ecological perspective.

Neophobia in Primate Field Studies

Perhaps the earliest report concerning neophobia in non-human primates comes from an account by Kawai (1960) on the translocation of a troop of Japanese macaques (Macaca fuscata). Observers found that although the animals were released into an area that had previously supported a monkey population (thus was assumed to have sufficient natural food sources) these animals ate little of the local vegetation and were considered to be starving. The brief account describing their feeding behavior at this time does say the animals ate moss and a plant stem (Eurya japonica) that the researchers considered inedible (Kawai, 1960). Provisioned food (sweet potatoes) was available that the animals eventually ate but it is unclear how close to the researchers the animals had to get for access to this food source. [For example, Kawai describes a researcher "offering" a sweet potato to individual animals which may indicate that they attempted to hand feed the animals (Kawai, 1960)].

Biswas, Medhi, & Mohnot (1996) described the behavior of a pair of golden langurs (Presbytis geei) introduced to a small island in Assam, India. The authors described the island's vegetation as being 70 to 80 percent different from where the animals originated (apparently in regard to the available flora). Of the leaves, fruits, and flowers the monkeys ate from the island vegetation, Biswas et al (1996) reported that they ate only the four or five species that had been present in their original home range. It should be noted that visitors to a temple on this small island supplement the monkeys' diet with food handouts.

In contrast, Silver & Ostro (1996) reported on the feeding habits of two troops of translocated black howler monkeys (Aloutta pigra) in Belize. Again the vegetation of the troops' new location was described as being composed of plant species that differed from the troops' original home range by 70 percent. Though newly translocated monkeys used fewer trees for feeding and fed less then troop members that had lived in the area for a year, prior experience with food species had little effect on diet selection (Silver & Ostro, 1996). These results might be explained by howler monkeys' ability to select particular leaves to eat based on taste alone (Glander, 1981).

Another account by Fedigan (1991) described a troop of Japanese macaques that was moved from Japan to Texas. These animals were described as being "fearless, innovative, and eclectic in what they would eat, sampling nearly all the local flora soon after arrival," (Fedigan, 1991, p. 60). Unfortunately it is not clear whether animals sampled small amounts of the new foods first, as would be expected with poison testing behavior, and no information is provided concerning the list of foods the animals did not eat.

This account of the Arashiyama macaques led Visalberghi (person. comm.) to suggest that neophobia may be abandoned under circumstances where the environment is completely different from what the animals are used to. Once a new diet is established, the animals may revert back to being neophobic. However, the Texas macaques are currently provisioned and no doubt had experience with commercial monkey chow before and immediately after their release. Therefore these monkeys' lack of food neophobia is still puzzling but impossible to resolve without more precise data.

Perception of Sweetness

Psychophysiological data are available for some New World monkeys concerning their ability to perceive substances that taste sweet to humans (Glaser, Tinti, & Nofre, 1996; Laska, 1997; Laska, Sanchez, Rivera, & Luna, 1996). For example, New World primates, including Cebus apella, do not perceive aspartame (Glaser et al, 1996) and squirrel monkeys show sugar preferences similar to humans in that they prefer sucrose (Laska et al, 1996). Test foods used in the experiments proposed here will include sucrose and other food associated sugars (those found naturally in fruits and vegetables). So far no sweetener has been identified that tastes sweet to humans but does not elicit a similar response in apes and old World primates (Hellekant & Danilova, 1996). This lends support to the claim that the sugar contained in the test foods in experiment five was detectable by the macaques.

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