SOCIAL TRANSMISSION OF FOOD PREFERENCES IN NORWAY RATS

THE SOCIAL TRANSMISSION OF FOOD PREFERENCES

IN

SMALL COLONIES OF NORWAY RATS

By

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ABSTRACT

The present research investigates the social transmission of food preferences in small colonies of domestic rats. In Experiment 1, four demonstrator rats were poisoned for consumption of a particular flavored diet and placed in a floor enclosure with a choice between the averted diet and an alternative diet. These original demonstrators were replaced one by one each 24-hr over a period of 4 days with naive subjects. The original demonstrators effectively transmitted a preference for the alternative diet to the naive replacements, as these replacements exhibited a preference for the alternative diet for a period of 4 days following the departure of the final demonstrator.

Employing essentially the same methodology as that used in Experiment 1, videotape analysis of the feeding behavior of subjects on the sixth day (zero original demonstrators, four naive replacements) of Experiment 2 revealed no significant difference in the food choices of the first, second, third and fourth replacement subjects, indicating that naive replacements became effective demonstrators following interaction with original demonstrators.

Random placement of the food bowls each day during Experiment 3 revealed that the social transmission of food preferences from original demonstrators to naive replacements can persist in the absence of excretory cues around a particular feeding site.

In Experiment 4, removal of demonstrators from the floor enclosure during periods in which foods were available there for replacement subjects to choose

between revealed that naive observers could obtain sufficient information from demonstrators during non-consumption periods to guide their food choices. Observers in Experiment 4 exhibited a preference for their respective demonstrators' diets when presented a choice between their demonstrators' diet and an alternative diet in the absence of demonstrators.

In the General Discussion, variables were discussed that might modify the strength of socially transmitted food preferences in rats and could be examined in future research using the present paradigm.

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GENERAL INTRODUCTION

Social Learning in *Homo sapiens*

In a consideration of social learning and the formation of cultural traditions in *Homo sapiens*, Jacobs and Campbell (1961) investigated the perpetuation of an arbitrary tradition in a social group which transcended the replacement of individual group members. The tradition investigated by Jacobs and Campbell concerned individual perceptions of autokinetic movement. When placed in a dark room, an individual will perceive movement while observing a stationary point of light. The first step in the Jacobs and Campbell experiment involved establishing an arbitrary tradition concerning the perceived extent of movement of the small point of light. Jacobs and Campbell placed a number of confederates in the darkened room to establish a tradition, who claimed to perceive very large movements of the light; they then replaced the confederates one by one with naive observers. The researchers referred to this small group of individuals as a microculture, a manageable laboratory situation in which to examine the behavior of natural human cultures.

Jacobs and Campbell considered the autokinetic illusion rather labile and expected that an arbitrary tradition, once established in a group, would be transmitted indefinitely without diminution. According to Jacobs and Campbell (1961):

> Once well indoctrinated, the naive group members would become as rigid and reliable spokesmen for the norm as were the confederates who proceeded them; that each new generation would unwittingly become a part of a self-perpetuating cultural conspiracy propagating superstition and falsehood

(p. 650).

Although the research did not demonstrate the expected rigid conformity to the established tradition, the arbitrary behavior did survive total replacement of the original confederates, and observations of indoctrinated observers did not return to levels of a control group for four to five generations (complete replacement of the original demonstrators followed by complete replacement of four to five sets of indoctrinated observers).

Social Learning in Animals

Although the process of social transmission of tradition appears rather pervasive in *Homo sapiens*, the question of social learning in animals has been the subject of a significant amount of debate. The primary examples of social transmission of local traditions concern sweet potato washing by Japanese macaques and termite fishing by chimpanzees. These anecdotal observations remain controversial, as researchers often disagree about appropriate definitions of culture and tradition. The definition of tradition for the present research follows Galef (1988), defining a traditional behavior as a behavior learned from local conspecifics and transmitted to naive individuals. The research presented in the following paper considers the social transmission of food preferences in small colonies of female Norway rats (*Rattus norvegicus*).

EXPERIMENT 1: FULL REPLACEMENT MICROCULTURE

Introduction

Discussion of the social transmission of local traditions in rodents dates to anecdotal observations by Steiniger (1950). Steiniger claimed that a poisoned bait placed in a rat infested area would not be effective in eliminating rodents over an extended period of time. In particular, Steiniger observed that the offspring of adult rats that survived poisoning rejected the toxic bait without having any contact with it. Steiniger proposed that the adults persuaded the offspring to avoid the poisoned bait by marking the site with their urine.

The anecdotal observations offered by Steiniger provided a research paradigm for laboratory experiments in the social transmission of food preferences. Research performed by Galef and colleagues has demonstrated several mechanisms each of which appears sufficient for the transmission of information concerning food preferences from one rat to another. These mechanisms include flavour cues transmitted through a mother's milk to her offspring (Galef & Clark 1972; Galef & Henderson 1972; Galef & Sherry 1973) and reception of olfactory cues from a conspecific demonstrator (Galef & Wigmore 1983). More recently, Laland and Plotkin (1991; 1993) have demonstrated that rats prefer to consume food from a site marked with excretory deposits.

The next logical step in the research on social transmission of food preferences involves establishing a controlled rodent microculture in a laboratory environment. Although research indicates that rats demonstrate an enhanced preference for foods consumed by a demonstrator, a majority of this research involves simple one-on-one interaction followed by a period of consumption by the observer in the absence of the demonstrator or other conspecifics.

The present experiment attempts to synthesize the research concerning social transmission of food preferences and the perpetuation of an arbitrary tradition through multiple generations of a laboratory microculture. In Experiment 1, the research methodology employing confederates and their gradual replacement by naive observers designed by Jacobs and Campbell (1961) serves as a model to investigate the social transmission of food preferences in Norway rats.

The laboratory microculture used in the present experiment consisted of four female Norway rats poisoned with lithium chloride for the consumption of either cayenne-flavored diet (Diet CAY) or wasabi-flavored diet (Diet WAS). Following injection, the original colony of demonstrators was placed in a floor cage with an ad libitum choice between Diet CAY and Diet WAS. After 24-hr of interaction and consumption, one demonstrator was removed and replaced by a naive observer, followed by another 24-hr of ad-libitum interaction and consumption of the two diets.

Removal of the original demonstrators proceeded one by one each 24-hr until only naive observers remained. The measurement of relative consumption of the averted and alternative diets (averted diet refers to the diet for which the original demonstrators were poisoned) tracked the social influence on food preference over the 8 days of the experiment.

Method

Subjects

Sixty-four female Long Evans rats, 48-56 days of age, acquired from the McMaster colony, and descended from Long-Evans stock acquired from Charles River, Canada (St. Constant, Quebec), served as original demonstrators in the present experiment. An additional 64 experimentally naive females, 48-56 days of age, born in the McMaster colony, served as observers.

Apparatus

Demonstrators were individually housed in wire-mesh hanging cages throughout the 2-day training period. Observers were housed in groups of four in a separate room in shoe-box cages prior to placement in floor enclosures.

Procedure

The procedure may be divided into two sections: (1) preparation of original demonstrators for the microculture and placement of these demonstrators in floor enclosures and (2) subsequent replacement of original demonstrators with naive observers.

Preparation of original demonstrators for the microculture proceeded as follows:

1. Demonstrators were randomly assigned to two different experimental groups (Diet CAY and Diet WAS). Demonstrators in the Diet CAY

group would be poisoned for consumption of Diet CAY while demonstrators in the Diet WAS group would be poisoned for consumption of Diet WAS.

2. Each demonstrator was placed in a wire-mesh hanging cage and maintained for 24-hr on ad-lib water and Purina Rodent Laboratory Chow pellets.

3. Each demonstrator was then food deprived for 23-hr so that it would eat a novel diet when one was made available.

4. Following food deprivation, four demonstrators were offered a weighed sample of Normal Protein Test Diet (Harlan Teklad, catalogue # 170590, Madison, Wisconsin) adulterated either with 0.3% powdered cayenne pepper (McCormick Canada, London, Ontario) (Diet CAY) or 2.5% powdered Wasabi, a Japanese horseradish used to prepare sushi (Mitoku Company Ltd., Tokyo, Japan) (Diet WAS). Results of a prior pilot study indicated that Diet CAY and Diet WAS were roughly equipalatable.

5. Immediately following completion of the 1-hr feeding period, each demonstrator was injected i.p. with 2% body weight 1% w/v LiCl solution. The demonstrators were then returned to their individual cages, given two pellets of Purina Laboratory Rodent Chow and allowed to recover for a period

of 23-hr.

6. Following the 23-hr recovery period, the demonstrators were offered another weighed sample of flavored Normal Protein Test Diet. Each subject received the same flavor that it had received on the previous day.

7. Immediately following the completion of the 1-hr feeding period, any demonstrator that had consumed the averted diet was again injected i.p. with 2% body weight 1% w/v LiCl solution. Demonstrators that failed to consume any averted diet received no injection. This procedure served as a fail-safe mechanism to ensure that original members of the microculture were indeed averted to a particular diet. Following the 1-hr feeding period and subsequent injections where necessary, demonstrators were returned to their individual cages with two Purina Laboratory Rodent Chow pellets and allowed to recover for a period of 23-hr.

8. Following the 23-hr recovery period, the four demonstrators that had been poisoned after consuming Diet CAY were numbered 1-4 with permanent marker on a white portion of their tails and placed together in a wire-mesh floor enclosure (see Figure 1) (96cm x 96cm x 33cm). The floor enclosure contained a small wooden nest box (32cm x 32cm x 18cm) with two entrances, two water bottles and two ceramic bowls (15cm diameter x 5cm

depth).

One food bowl contained a weighed sample of Diet CAY, while the other contained a weighed sample of Diet WAS. The positions of the food bowls were counterbalanced across floor enclosures to avoid placement effects. The four remaining demonstrators that were assigned to the Diet WAS group were marked in a similar manner to the Diet CAY demonstrators were placed in a separate floor enclosure with similar specifications and food bowls.

The two floor enclosures were separated by sheet metal barriers to prevent any visual or physical contact between the demonstrators in the two enclosures. The demonstrators were allowed a 24-hr period of interaction and ad libitum food consumption.

Insert Figure 1

Once the original demonstrators had spent 24-hr in their respective floor enclosures, replacement of demonstrators proceeded as follows:

1. At the end of the 24-hr period of interaction, the food bowls were weighed

to determine the relative consumption of Diet CAY and Diet WAS by each group of demonstrators. The demonstrator marked #1 was removed from each floor enclosure and replaced with a naive observer marked #1 with permanent marker. The flavored food in each food bowl was replenished, followed by another 24-hr period of interaction and ad-lib food consumption.

2. This removal process proceeded for 3 additional days, with the demonstrator identified as #2 removed and replaced with a naive observer on the second day, the demonstrator identified as #3 removed and replaced with a naive observer on the third day and the demonstrator identified as #4 removed and replaced with a naive observer on the fourth day. Food bowls were weighed and replenished each day.

3. The four observers were allowed ad lib food consumption and unobstructed interaction for an additional period of 3 days. The only disturbance involved daily measurement and replenishment of food bowls. Following the completion of the 3-day period, observers were removed from floor enclosures.

Results

To determine if transmission of an arbitrary food preference survived complete replacement of the original colony, mean percentages of Diet CAY consumed on the fifth, sixth, seventh and eighth days of the experiment by each microculture were analyzed with a repeated measures ANOVA. While the information from the first 4 days may appear interesting, this information is theoretically uninformative as in each of these days at least one member of the microculture had received lithium chloride injections for consumption of an averted diet, and only total consumption by all members of the microculture was obtained. The analysis of variance revealed that social transmission of an arbitrary food preference survived complete replacement of original colony members, as the observers still preferred the alternative diet after complete removal of original demonstrators ($F(1,15)14.04$, $p<0.05$) (Figure 2).

Insert Figure 2

Discussion

The results of Experiment 1 indicate that social transmission of food preferences can survive replacement of original colony members. Despite the fact that naive observers lacked prior information concerning diets available in the floor enclosure, they continued to exhibit a preference for the alternative diet following removal of all original demonstrators. However, information obtained from Experiment 1 does not confirm the anecdotal evidence provided by Steiniger (1951).

Although naive observers exhibited a preference for the alternative diet, they did not completely avoid the averted diet.

The finding that naive observers do not completely avoid the averted diet raises the question as to which naive observer(s) actually consumed the averted diet. At the extremes, perhaps each naive observer consumed the averted diet in a 20%/80% ratio with the alternative diet, or perhaps one naive observer consumed the averted diet in an 80%/20% ratio while the remaining naive observers remained faithful to the original aversion. The experimental design in Experiment 1 offers only a gross measurement of total consumption of the averted and alternative diets by the entire colony (demonstrators and/or naive observers) so the answer to this question requires an alteration in experimental methodology.

EXPERIMENT 2: VIDEOTAPE ANALYSIS

Introduction

To discern which naive observers actually consumed averted diet, minor alterations were made to the original procedure, and consumption periods on the sixth day of the experiment were recorded on time lapse videotape and analyzed. The sixth day was chosen for analysis because preliminary videotapes indicated that the fourth naive replacement often did not consume any food on the fifth day. The fourth replacement spent a significant amount of time investigating the floor enclosure and grooming remaining observers.

The primary objective of the videotape analysis concerned the issue of fidelity to the original aversion by naive replacements. While the first naive replacement interacts with three original demonstrators, the final naive replacement never interacts with any original demonstrators. The videotape analysis indicated whether the number of original demonstrators with which a naive observer interacted affected subsequent fidelity of naive observers to avoidance of averted diets.

Method

Subjects

Forty experimentally naive, female Long-Evans rats, 48-56 days of age, born and raised in the McMaster colony, and descended from Long-Evans stock acquired from Charles River, Canada (St. Constant, Quebec), served as original demonstrators in the present experiment. An additional 40 experimentally naive females, 48-56 days of age, acquired from the McMaster colony served as naive observers.

Procedure

The procedure for Experiment 2 was identical to the procedure from Experiment 1 with the following exceptions:

1. The consumption period in floor cages was reduced from 24-hr ad-lib feeding to a 3-hr feeding period. This reduction in feeding time made videotape analysis manageable, while allowing demonstrators and observers in floor enclosures to obtain an adequate amount of food in

24-hr periods.

2. Replacement of original demonstrators occurred immediately following termination of the 3-hr consumption period on each day, allowing the naive replacements an opportunity to integrate into the colony for 21-hr prior to the start of another 3-hr consumption period.

3. The length of floor-cage trial periods was reduced from 8 to 6 days as the additional 2 days did not appear relevant to the question at hand.

Results

A repeated measures ANOVA of the mean percentage Diet CAY consumed on the fifth and sixth days revealed that the social transmission of the arbitrary food preference once again survived complete replacement of original demonstrators ($F(1.9)=1054.7$, $p<0.05$)(Figure 3).

Insert Figure 3

A repeated measures ANOVA for the fifth and sixth days between Experiment 1 and Experiment 2 revealed that the reduction in consumption time from 24-hr to only 3-hr enhanced the observers' preference for alternative diet (Diet CAY original demonstrators: $F(1,12)=10.57$; $p<0.05$; Diet WAS original demonstrators: $F(1,12)=12.13$; $p<0.05$).

Videotape analysis of the consumption period registered the amount of time (minutes and seconds) that each observer spent at each food bowl. Only periods of longer than 3 sec were recorded. Recorded time began when the nose of an observer passed over the edge of a food dish and lasted until the nose of the observer left the food dish. Time spent grooming, sniffing the sides of the food dish or digging at the wood shavings around the food dish were not recorded.

An analysis of the time spent by the naive observers at the averted food site reveals that the number of original demonstrators present when the naive observer entered the floor enclosure was not significantly associated with the time spent by each naive observer at the averted food site (Kruskal-Wallis for Diet CAY Averse $H=5.27$, Kruskal-Wallis for Diet WAS Averse $H=4.55$, H critical=7.82) (Figure 4). This analysis indicates that the time spent at the averted food site by first naive replacements (three original demonstrators) did not significantly differ from the time spent at the averted food site by final naive replacements (no original demonstrators).

Insert Figure 4

An analysis of the correlation between the time spent at the Diet CAY food site and total Diet CAY consumption revealed a significant correlation (r=0.992)(Figure 5).

Insert Figure 5

Discussion

The absence of a significant difference in time spent at the averted food bowl among the four replacements indicates that once indoctrinated, a naive replacement becomes an effective demonstrator for the next naive replacement. While naive replacements may not avoid the averted diet as faithfully as did original demonstrators, the fourth replacement never interacted with original demonstrators. Consequently, the fourth replacement would consume the novel, equipalatable diets at chance levels unless information obtained from the first three replacements indicated that the alternative diet was preferred to the averted diet. The information obtained from this experiment appears to coincide with the results from the autokinetic illusion experiment performed by Jacobs and Campbell; naive observers became as rigid and reliable spokesmen for the norm as were the original confederates.

The enhanced preference for the alternative diet in Experiment 2 indicates that time constraints placed on the availability of food exert a powerful influence on the social transmission of food preferences. The restriction of time might reduce random sampling of the environment by the naive observers essentially limiting these observers to the information provided by experienced conspecifics.

EXPERIMENT 3: RANDOM PLACEMENT MICROCULTURE

Introduction

In an investigation of social transmission of food preferences in Norway rats, Laland and Plotkin (1993) observed that rats consistently prefer to feed from a food bowl marked by excretory products from conspecific demonstrators rather than from a similar food bowl without these excretory deposits. The researchers concluded that the combination of urine and fecal deposits around a particular feeding site rendered that site attractive to naive observers and that excretory deposits alone appear sufficient for the social transmission of food preferences. The third experiment was undertaken to determine if demonstrator rats can communicate food preferences to naive observers in the absence of excretory deposits around a particular feeding site. While Laland and Plotkin determined that excretory deposits are sufficient for the social transmission of food preferences, this experiment should determine if excretory deposits are necessary for social transmission.

Method

Subjects

Thirty-two experimentally naive, female Long-Evans rats, 48-56 days of age, born and raised from the McMaster colony and descended from Long-Evans stock acquired from Charles River, Canada (St. Constant, Quebec) served as original demonstrators. An additional thirty-two experimentally naive females 48-56 days of age, acquired from the McMaster colony served as naive replacements.

Procedure

The procedure for Experiment 3 was identical to that of Experiment 2 with the following exceptions:

1. Rather than the simple, counterbalanced food bowl placement used in prior experiments, the position of the food bowls changed each day (Figure 6). The position of food bowls was determined prior to the experiment using a random number table. The random placement of each food bowl on each individual day ensured that any excretory deposits from the previous day would be of little help for naive observers.

Insert Figure 6

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2. Following the termination of the 3-hr consumption period, all surfaces of each food bowl were cleaned to remove urine or fecal deposits and all fecal deposits were removed from each food bowl. The food bowls were replenished to cover any remaining excretory deposits left inside the food bowls.

3. Following the consumption period on day 6, the naive observers were removed from their floor enclosures and placed in individual wire-mesh hanging cages with only a water bottle. The observers were food deprived until the next day, when at the normal feeding time, a weighed sample of Diet CAY and a weighed sample of Diet WAS were placed in each cage. The observers were allowed a 3-hr consumption period. After the 3-hr consumption period, the food cups were removed and weighed to determine relative consumption. This post-enclosure test determined if naive observers retained their preferences for alternative diets.

Results

A repeated measures ANOVA of the relative consumption on the fifth and sixth days of the experiment revealed that the social transmission of food preferences from original demonstrators to naive observers persisted in the absence of excretory deposits surrounding particular feeding sites ($F(1,7)=59.78$, $p<0.05$) (Figure 7).

Insert Figure 7

A Mann-Whitney U test of diet choice of naive observers in the individual wire-mesh cages revealed a significant difference in the consumption of Diet CAY between experimental groups (Diet CAY and Diet WAS) for the first, second and fourth replacements (first replacement U=0; p=0.014, second replacement U=0; p=0.014, fourth replacement U=0; p=0.014). No significant difference appeared between the experimental groups (Diet CAY and Diet WAS) for the third replacement (U=3; p=0.1)(Figure 8). A Kruskal-Wallis analysis of diet choice by naive observers in individual wire-mesh cages revealed no significant difference in consumption by naive replacements within the experimental groups as a function of the number of original demonstrators present when the naive observer entered the floor enclosure (CAY averse H=0.76, WAS averse H=1.68, H critical = 7.82).

Insert Figure 8

Discussion

Although the research performed by Laland and Plotkin (1993) demonstrated that excretory deposits are sufficient for social transmission of food preferences, these excretory deposits do not appear to be necessary for social transmission. Excretory deposits appear to function as one of several redundant cues by means of which rats can obtain information from conspecifics concerning a distant food site.

The failure to find a significant difference in consumption of Diet CAY in the post-floor-enclosure individual tests for the third replacements remains a mystery, as the fourth replacements demonstrated a significant difference in Diet CAY consumption. If the fourth replacements failed to demonstrated a significant difference in consumption of Diet CAY, it would indicate that the later replacements do not retain the socially transmitted information concerning diet preference. Since the fourth replacements demonstrate a significant difference in consumption, the failure to find significance with the third replacements may result from small sample size.

EXPERIMENT 4: OBSERVERS ONLY

Introduction

In Experiment 2, the preliminary videotape analysis of relative consumption on the fifth day revealed that the fourth replacement often followed conspecifics to a particular food dish but did not consume any food. Rather, the fourth replacement groomed conspecifics and investigated wood shavings surrounding the food dish. Perhaps the physical presence of conspecifics around a particular food dish served as local enhancement for a naive observer (Thorpe, 1963). This local enhancement could play an important role in the social transmission of food preferences from original demonstrators to naive observers, if each naive observer spent the first day in the floor enclosure simply observing experienced conspecifics. Excretory deposits and reception of olfactory cues from conspecifics would appear to be redundant, auxiliary mechanisms if the naive observer only need watch conspecifics consume from a particular feeding site in order to determine the food preferences of conspecifics.

Experiment 4 examines the role of the physical presence of experienced conspecifics in the social transmission of food preferences in a small colony of Norway rats. Instead of providing the opportunity for naive observers to feed with original demonstrators, these demonstrators spent 3-hr outside the floor enclosure in individual wire-mesh cages consuming a particular diet (Diet CAY or Diet WAS) and were allowed to interact with naive observers only during non-consumption periods.

Method

Subjects

Twenty-four experimentally naive, female Long-Evans rats, 48-56 days of age, born and raised in the McMaster colony and descended from Long-Evans stock acquired from Charles River, Canada (St. Constant, Quebec) served as original demonstrators. An additional twenty-four experimentally naive females 48-56 days of age, served as naive observers.

Apparatus

The floor enclosure used in Experiment 4 had the same arrangement as the floor enclosure used in Experiment 1 (Figure 1) with the nest box placed in the far right corner of the enclosure and the food bowls placed in far-left and near-right corners, equidistant from the nest box. The placement of the food bowls was counterbalanced across enclosures for the duration of the experiment. Original demonstrators were housed during the 3-hr feeding period in individual, wire-mesh hanging cages like those described in Experiment 1.

Procedure

1. Demonstrators were randomly assigned to two different experimental groups (Diet CAY and Diet WAS) . The demonstrators were placed on a feeding schedule, eating Purina Laboratory Rodent Chow for 3-hr per day for 2 days. Naive observers were randomly assigned to two different experimental groups (Diet CAY and Diet WAS) and maintained on a 3-hr feeding schedule with Purina Laboratory Rodent Chow until placed in floor enclosures.

2. On the third day, three demonstrators were offered a weighed sample of Normal Protein Test Diet adulterated with 0.3% powdered cayenne (Diet CAY), while the remaining three demonstrators were offered a weighed sample of Normal Protein Test Diet adulterated with 2.5% powdered wasabi (Diet WAS).

3. Following the 3-hr consumption period, the three Diet CAY demonstrators were placed in a floor enclosure with one naive observer while the three Diet WAS demonstrators were placed in a separate floor enclosure with one naive observer. The floor enclosure contained only a nest box and two water

bottles. No food bowls were present in the floor enclosure.

4. The three demonstrators and one observer were allowed to interact for a period of 21-hr.

5. Following the 21-hr interaction period, the three demonstrators were removed from the floor enclosure. Two demonstrators were placed back in wire-mesh hanging cages and offered a weighed sample of either Diet CAY or Diet WAS. Each observer received the same diet that it had received on the previous day. The demonstrators were allowed a 3-hr consumption period. The remaining demonstrator from each floor enclosure was discarded.

6. The naive observer left in each floor enclosure received weighed samples of Diet CAY and Diet WAS placed in food bowls at opposite corners of the floor enclosure was allowed a 3-hr period of consumption.

7. Following the termination of the 3-hr consumption period, the food bowls were removed from the floor enclosure and were weighed to determine relative consumption. The demonstrators were removed from the individual cages and returned to the floor enclosures along with an additional naive observer for each floor enclosure. The two demonstrators

and two observers were allowed to interact for 21-hr with only a nest box and water bottles.

8. Following the termination of the 21-hr period of interaction, the two demonstrators were removed from each floor enclosure. One demonstrator from each enclosure was placed in an individual hanging wire-mesh cage and offered a weighed sample of adulterated Normal Protein Test Diet (Diet CAY or Diet WAS) for a 3-hr period. Each observer received the same diet it had received on previous days. The remaining demonstrator from each floor enclosure was discarded.

9. The two observers in each floor enclosure received a weighed sample of Diet CAY and Diet WAS for a 3-hr period. The food bowls were placed in the same corner in which they had been placed on the previous day.

10. Following the termination of the 3-hr feeding period, the food bowls were removed from each floor enclosure and weighed to determine relative consumption. The demonstrators were removed from individual cages and placed in their respective floor enclosures along with an additional naive observer. The single demonstrator and three observers were allowed to interact for a 21-hr period.

11. Following the termination of the 21-hr period of interaction, the remaining demonstrator from each floor enclosure was removed and discarded. The three observers were offered a weighed sample of Diet CAY and Diet WAS for a 3-hr period. The position of the food bowls remained consistent with previous days.

12. At the end of the 3-hr feeding period, the food bowls were removed and weighed to determine relative consumption, and the three observers were allowed a period of 21-hr to interact in the absence of any demonstrators.

13. At the end of the 21-hr period of interaction, the observers were offered a final 3-hr choice between weighed samples Diet CAY and Diet WAS, placed in the same position as previous days. These food bowls were weighed at the end of the 3-hr period to determine relative consumption.

14. Following the consumption period on the fourth day, the naive observers were removed from the floor enclosures and individually placed in wire-mesh hanging cages with only a water bottle. The observers were food deprived until the next day when, at the normal feeding time, a weighed sample of Diet CAY and a weighed sample of Diet WAS were placed in the cage. The observers were allowed a 3-hr consumption period. After the 3-hr

consumption period, the food cups were removed and weighed to determine relative consumption. This post enclosure test would determine if the naive observers retained the preference for their respective demonstrators' diets.

Results

A repeated measures ANOVA of the relative consumption of Diet CAY on the third and fourth days by the microcultures with cayenne demonstrators versus the microcultures with wasabi demonstrators revealed that the naive observers prefer the demonstrators' diet over the alternative diet ($F(1,7)=30.12$; $p<0.05$)(Figure 9).

Insert Figure 9

A Mann-Whitney analysis of post floor enclosure individual tests revealed a significant difference in the consumption of Diet CAY between the experimental groups (Diet CAY and Diet WAS) for the first, second, third replacements (first replacement $U=0$; $p=0.014$, second replacement $U=0$, $p=0.014$, third replacement $U=1$; $p=0.029$)(Figure 10). A Kruskal-Wallis analysis of post-floor-enclosure diet choice revealed no significant difference in consumption by naive replacements within the experimental groups (CAY demonstrators $H=0.27$, WAS demonstrators $H=0.04$, H critical = 5.99).

Insert Figure 10

Discussion

The results of Experiment 4 demonstrate that the physical presence of the original demonstrators was not necessary for social transmission of food preferences to naive observers. This indicates that naive observers obtained sufficient information concerning food preferences of demonstrators through olfactory cues present on the demonstrators during a non-consumption period. Naive observers needed to observe neither original demonstrators at a particular food site nor to follow original demonstrators to a particular food site. In addition, these results indicate that the naive observers obtained information from the original demonstrators, stored this information, and retrieved the information during consumption in the absence of the original demonstrators.

GENERAL DISCUSSION

A significant amount of theoretical discussion on the social transmission of food preferences in rodents concerns the ability of successful foragers to transmit information to less successful conspecifics. According to Galef (1991), an aggregation of unrelated rodents in a burrow may serve as an information center where conspecifics can exchange information concerning particular feeding sites. The research performed by Galef and colleagues indicates that the exchange of information may not follow the guidelines of reciprocal altruism outlined by Trivers (1985), e.g. research does not indicate that non-reciprocators can be identified or discriminated against. Instead, the exchange of information concerning distant feeding sites by rodents may involve an exploitative relationship where less successful foragers may obtain information from successful foragers. In addition, successful foragers may exchange information with successful conspecifics, which would increase the chance that both foragers would be successful in the future in the event that one particular feeding site disappeared. In an environment containing widely distributed resources, the exploitative exchange of information might provide a mechanism to increase individual fitness. The selective pressures exerted by the distribution of resources would appear to shape the mechanisms of social transmission.

Although the selective pressures exerted on rodents living in an environment with widely distributed resources certainly contributed to the mechanisms of social transmission of food preferences, perhaps an additional selective pressure helped to shape the mechanisms of social transmission. While the social transmission of information concerning distant food sites may assist less successful foragers, the process of social transmission will certainly assist new members in the avoidance of potentially noxious food sites.

Since the implication of rodents in the spread of the plague in the Middle

Ages, humans have attempted to control rodent populations to eliminate the plague and reduce the financial loss suffered when rodents destroy foodstuffs. The primary method employed to control rodent populations involved poisoning. Typically, this method involved luring rodents to a particular site with food which contained poison. To be successful in eliminating of rodents, humans needed to possess a fundamental knowledge of the feeding behavior of rodents. Rodents experienced a different problem. To be successful, rodents needed to avoid poisoned food sites. Thus, poisoning resulted in an escalating battle between cognizant humans and seemingly unsophisticated rodents. The selective pressures exerted by these control measures may have contributed to the redundant systems of social transmission as a method to avoid poisoned food sites. If rodents were not able to communicate information concerning safe feeding sites then simply placing zinc phosphate in palatable food would effectively eliminate an entire rodent population. But as Steiniger (1950) observed, zinc phosphate is not effective over a long period of time.

Regardless of theoretical perspective, to resolve any questions concerning the social transmission of food preferences, a distinction should be made between necessary and sufficient mechanisms. Laland and Plotkin (1991; 1993) determined that excretory deposits appear sufficient for the social transmission of food preferences, but the research performed in Experiment 3 indicates that excretory deposits are not necessary for social transmission. Perhaps the mechanisms of social transmission of food preferences contain a hierarchy of variables, some variables necessary and other variables sufficient.

Four different variables would appear important to an individual rodent placed in a floor enclosure in the paradigm described in this thesis:

Past experience with available diets

The mechanisms of neophobia and learned aversions will affect the diet selection of an individual rodent. Demonstrators poisoned with lithium chloride consumed significantly more of the alternative diet than of the aversive diet on the first day of Experiment 1. Typically, the four original demonstrators avoided an averted diet completely and consumed only the alternative diet. When faced with consuming the aversive diet, a novel alternative diet or starving, original demonstrators choose the alternative diet.

Direct information from conspecifics

In the absence of past experience with the available diets, naive observers appear to rely on information obtained from conspecifics. Three distinct cues may be obtained from conspecifics: olfactory cues, physical presence and flavour transmitted through milk to offspring. The research performed in the fourth experiment indicates that physical presence is not a necessary cue for the social transmission of food preference but physical presence may serve as an auxiliary cue for local enhancement. In addition, the size of the original colony, rate of replacement, sex and age of the original demonstrators may affect the feeding behaviors of the naive observers.

Indirect information from conspecifics: Excretory deposits

Laland and Plotkin determined that excretory deposits appear sufficient in the social transmission of food preferences. The research performed in these experiments indicates that excretory deposits may be a sufficient mechanism but not a necessary mechanism. Perhaps excretory deposits serve as a last resort in the absence of past experience or direct information from conspecifics.

Sundry physical variables

Distance to available food sites

Although not manipulated in these experiments, distance to the two food bowls may affect diet selection by both the original demonstrators and naive observers. If the alternative diet is placed in a distant or hidden location while the averted diet sits at the entrance to the nest box, the subsequent feeding behavior of the demonstrators and observers may favor the averted diet rather than starvation.

Time restrictions

One interesting side note to this research concerns the restriction of the consumption period from 24-hr to 3-hr following the first experiment. At first glance, this restriction and the subsequent enhancement of social transmission of food preferences observed in the final three experiments would appear to be a laboratory artifact of questionable ecological validity. However, Barnett (1963) observed that time restrictions on the availability of food affect the consumption patterns of rodents in a natural environment. This does not seem surprising as consumption during particular times of the day may increase predation thus restricting consumption to a small portion of a 24-hr period.

Equipalatablity of the available diets

This variable seems quite obvious. If the demonstrators are poisoned for consumption of an extremely palatable food and left with a choice between this palatable, aversive diet and an extremely unpalatable novel diet, the demonstrators may attempt to consume the palatable, aversive diet to determine if this diet does indeed cause illness rather than consume the extremely unpalatable diet. Simply increasing the percentage of cayenne to 1% will create an extremely unpalatable diet. Preliminary research on the equipalatablity of cayenne and wasabi indicates that rats find a diet flavored with this level of cayenne to be extremely aversive.

Nutritive value of the available diets

Past research demonstrates that rodents can alter consumption patterns based on the absence of essential nutrients. Employing the methodology for the fourth experiment, demonstrators can feed independently on a flavored food with all essential nutrients and then demonstrate to naive observers offered a choice between the demonstrators' diet without the essential nutrients and an alternative diet with all essential nutrients to determine if the observers will continue to consume the demonstrators' diet although this diet will contribute to illness. Preliminary research performed in the Galef laboratory indicates that the frequency of demonstration will affect the consumption patterns of an observer offered a choice between the demonstrators' diet without the essential nutrients and an alternative diet (Galef, unpublished).

The hypothesis that social transmission of food preference assists naive or less successful foragers in the avoidance of poisoned food sites suffers from one damaging piece of information. Research performed by Galef, Wigmore and Kennett (1983) failed in an attempt to demonstrate socially transmitted taste aversion learning. Surprisingly, naive observers prefer to consume a particular diet after interacting with an obviously ill demonstrator. This information would appear to devastate any hypothesis of social transmission which involved the transmission of poison avoidance. All of the information appears to be available to the observer: olfactory cues will indicate the food consumed by the demonstrator and the observer can personally learn an aversion to a noxious substance. However, this information cannot be synthesized by the observer. This information implies that poison avoidance cannot be the sole selective pressure shaping the social transmission of food preferences. If the selective pressure of poison avoidance shaped the social transmission of food preferences, then the social transmission of learned aversions would appear to be the primary mechanism in which to accomplish this task. Since this does not appear to be the case, a subtle combination of the selective pressures exerted by exploitative exchange of information concerning distant food sites and poison avoidance may have shaped the social transmission of food preferences in Norway rats.

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FIGURE CAPTIONS

Figure 1: A schematic of the floor enclosure design for Experiments 1, 2, and 4 including enclosure dimensions and placement of the nest box, food bowls and water bottles.

Figure 2: Results obtained from Experiment 1 expressed in percentage Diet CAY consumed by the experimental groups (Diet CAY demonstrators represented by squares and Diet WAS demonstrators represented by circles). Error bars indicate SEM. N=8 for Diet CAY. N=8 for Diet WAS.

Figure 3: Results obtained from Experiment 2 expressed in percentage Diet CAY consumed by the experimental groups (Diet CAY demonstrators represented by squares and Diet WAS demonstrators represented by circles). Error bars indicate SEM. N=5 for Diet CAY. N=5 for Diet WAS.

Figure 4: Results obtained from videotape analysis on the sixth day of Experiment 2 with the mean percentage time spent at the Diet CAY food dish displayed for all naive replacements in each experimental group. Error bars indicate SEM. N=5 for each naive observer in Diet CAY and Diet WAS.

Figure 5: The correlation between mean percentage time spent at the Diet CAY food bowl on day 6 by all observers in each experimental group and the percentage Diet CAY consumed on that day.

Figure 6: A schematic of the floor enclosure design for Experiment 3 with the placement of the nest box and water bottles along with a legend indicating placement of the food bowls on each day.

Figure 7: Results obtained from Experiment 3 expressed in percentage Diet CAY consumed by the experimental groups on each day. Error bars indicate SEM. N=4 for Diet CAY and N=4 for Diet WAS.

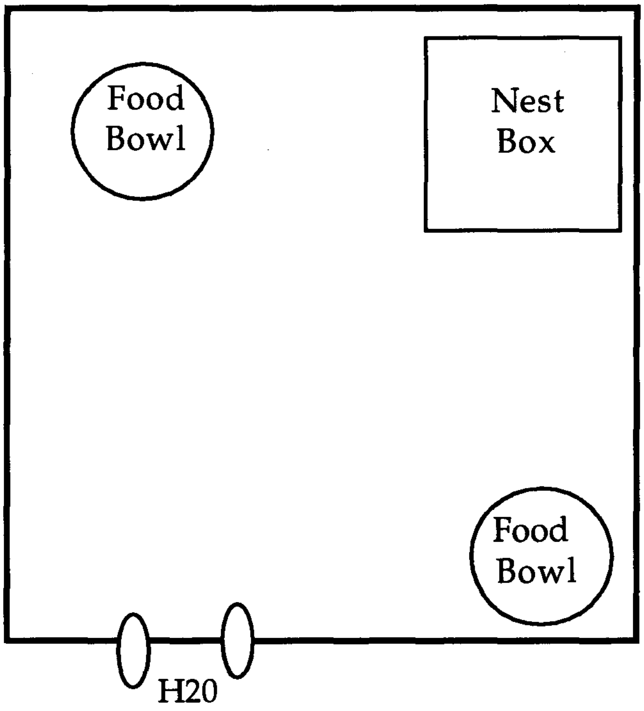
Figure 8: Results obtained from the post floor enclosure individual tests from Experiment 3 expressed as percentage Diet CAY consumed by each naive replacement. N=4 for each naive replacement in Diet CAY and Diet WAS. Error bars indicate SEM.

Figure 9: Results obtained from Experiment 4 expressed as percentage Diet CAY consumed by the experimental groups on each day. N=4 for Diet CAY and N=4 for Diet WAS. Error bars indicate SEM.

Figure 10: Results obtained from the post floor enclosure individual tests from Experiment 4 expressed as percentage Diet CAY consumed by each naive

observer. N=4 for each naive observer in Diet CAY and Diet WAS. Error bars indicate SEM.

Figure 1: Floor Enclosure Diagram

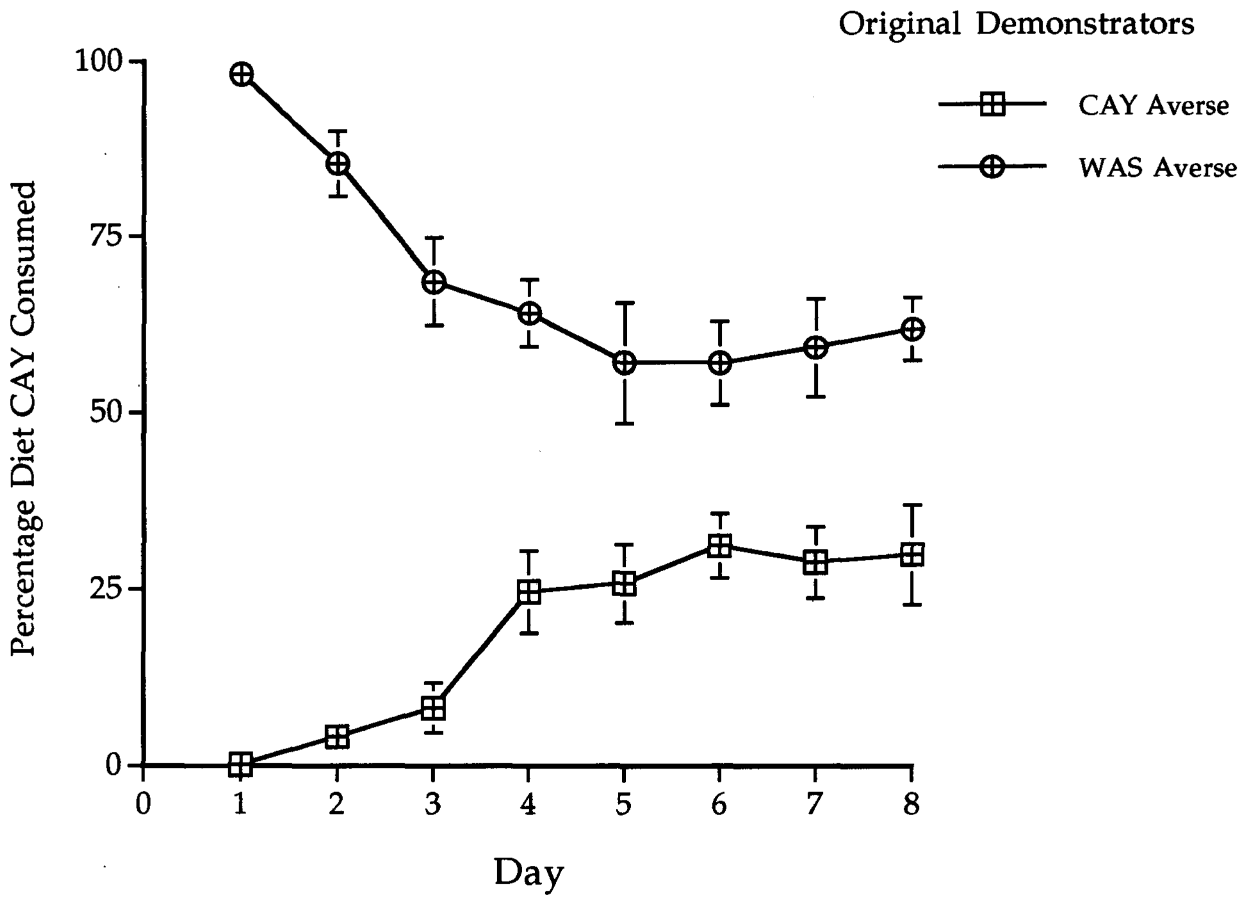


Floor Cage Dimensions:
Length: 96cm
Width: 96 cm
Height: 33cm

Food Bowl Dimensions:
Diameter: 15cm
Height: 5cm

Nest Box Dimensions
Length: 32cm
Width: 32cm
Height: 18cm

Figure 2: Full Replacement Microculture



Day 1: Four Demonstrators - Zero Observers
Day 2: Three Demonstrators - One Observer
Day 3: Two Demonstrators - Two Observers
Day 4: One Demonstrator - Three Observers
Days 5-8: Zero Demonstrators - Four Observers

Figure 3: Full Replacement: Videotape Microculture

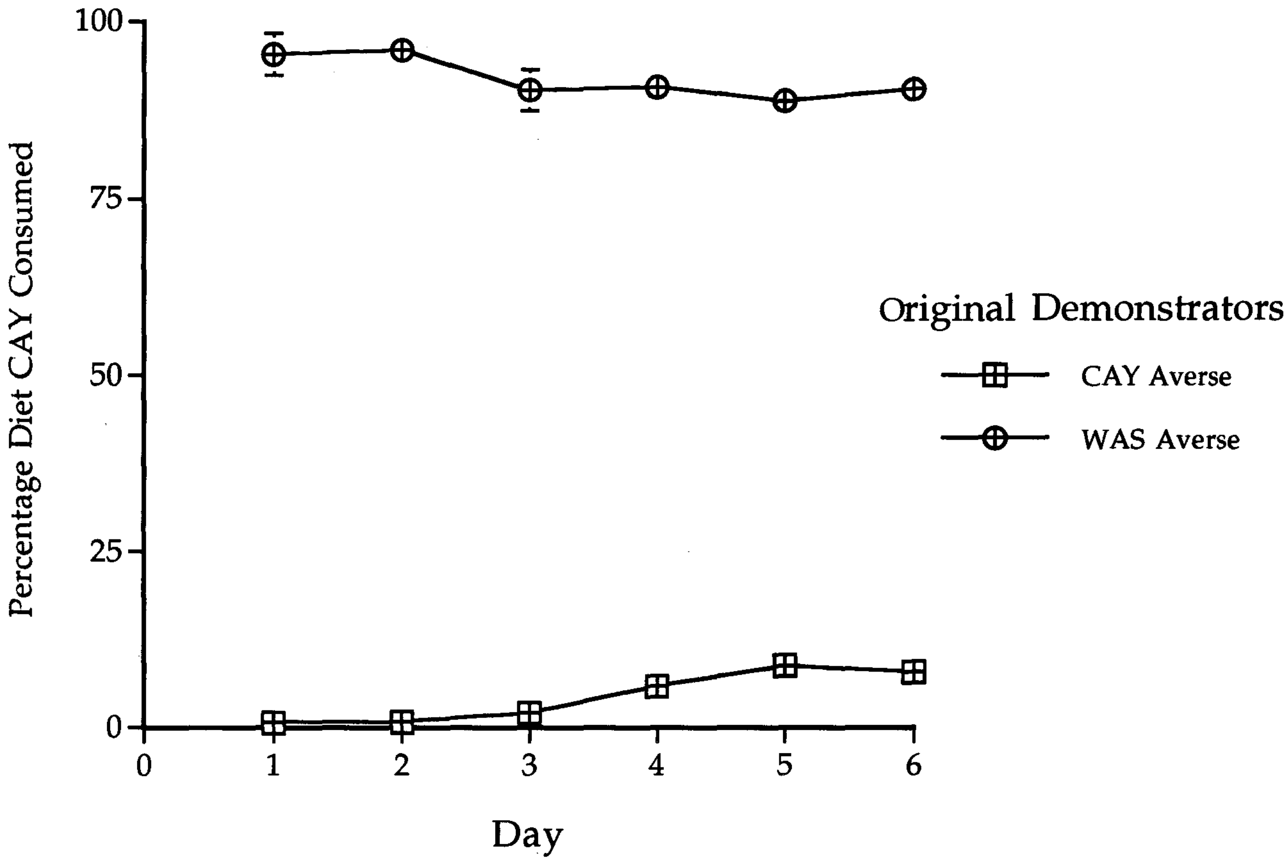


Figure 4: Time Spent at Cayenne Food Bowl

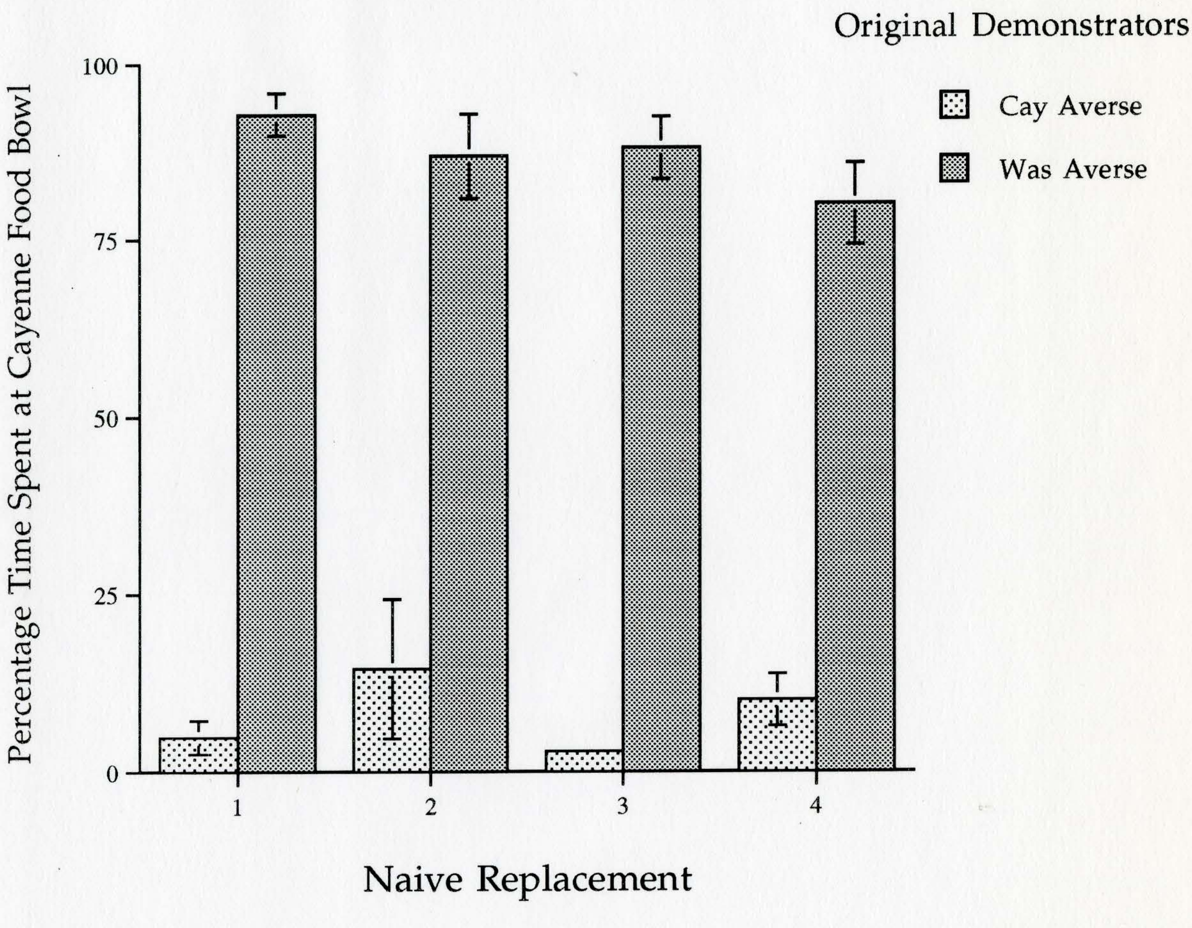


Figure 5: Correlation between Time and Consumption

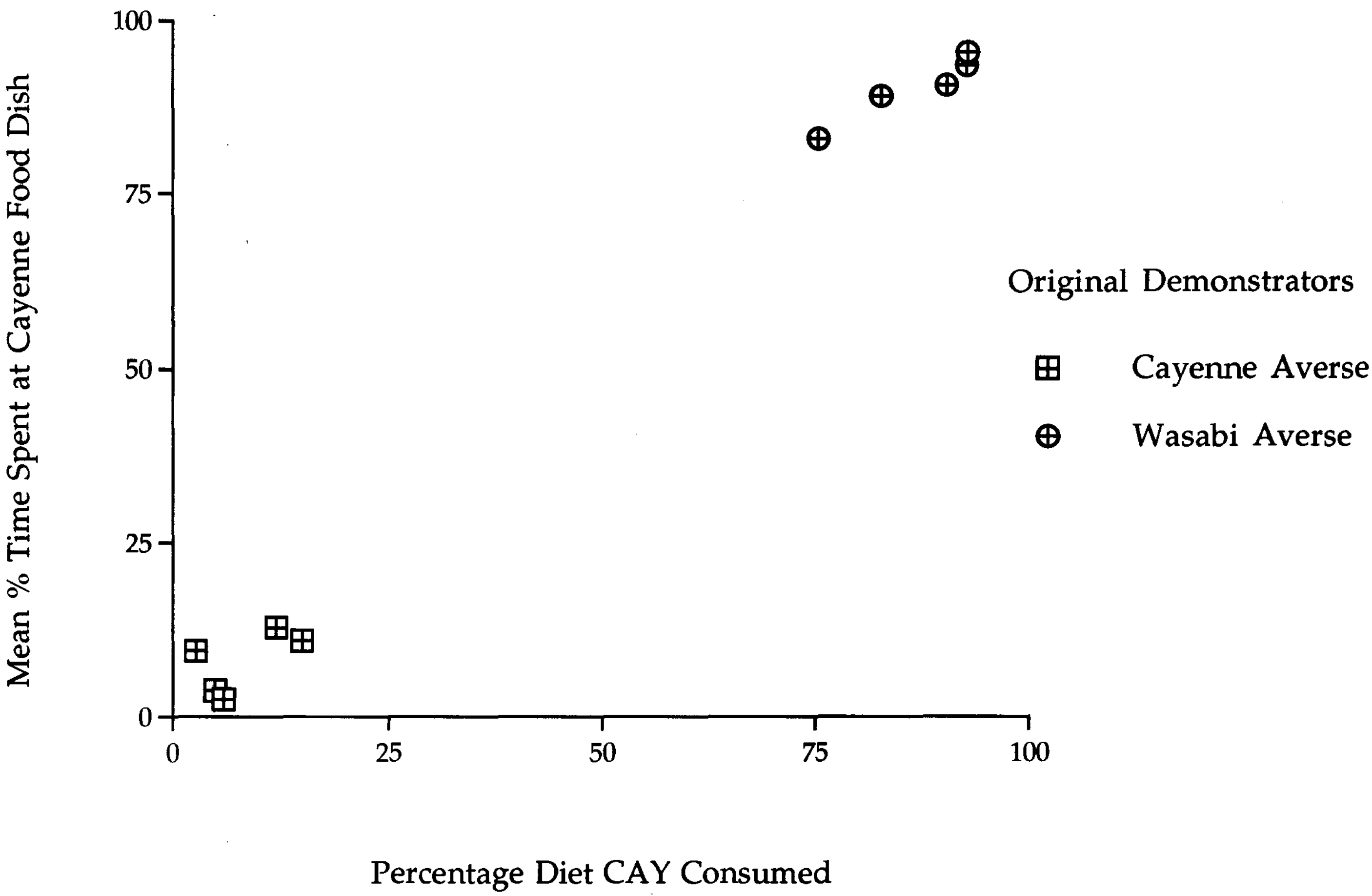
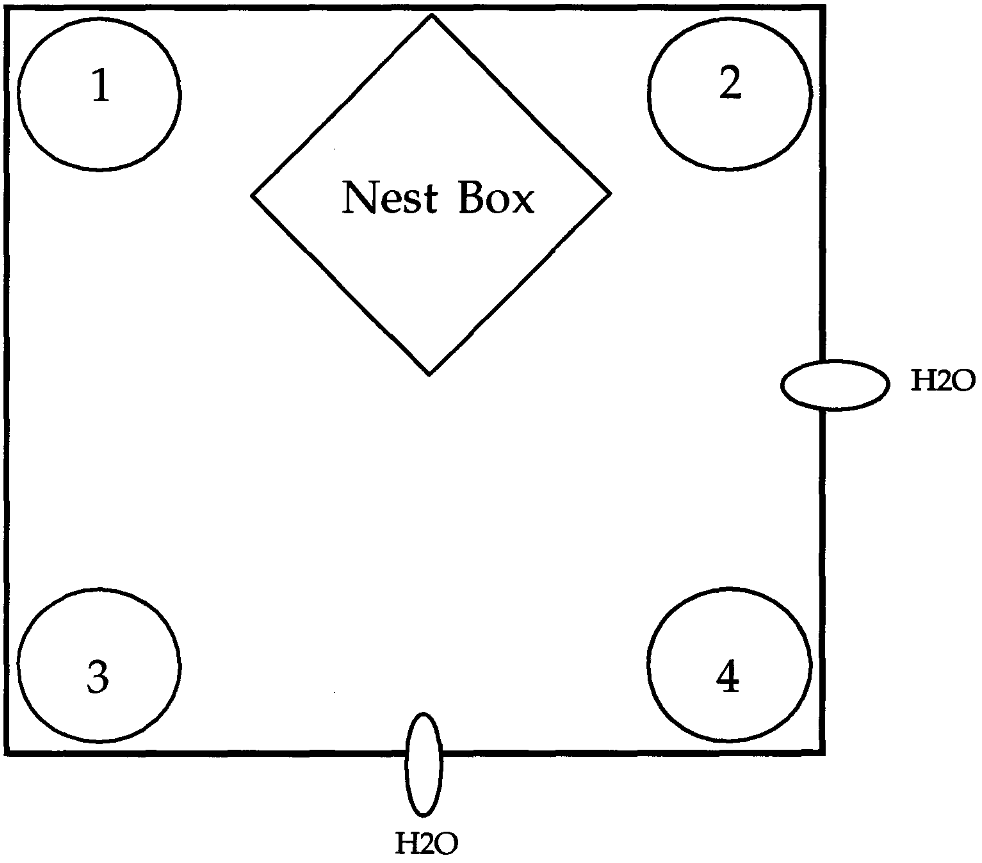


Figure 6: Random Placement
Enclosure



Food Bowl Placement
Day 1: Cayenne (1) - Wasabi (3)
Day 2: Cayenne (4) - Wasabi (2)
Day 3: Cayenne (3) - Wasabi (2)
Day 4: Cayenne (1) - Wasabi (4)
Day 5: Cayenne (2) - Wasabi (3)
Day 6: Cayenne (2) - Wasabi (4)

Figure 7: Random Placement Microculture

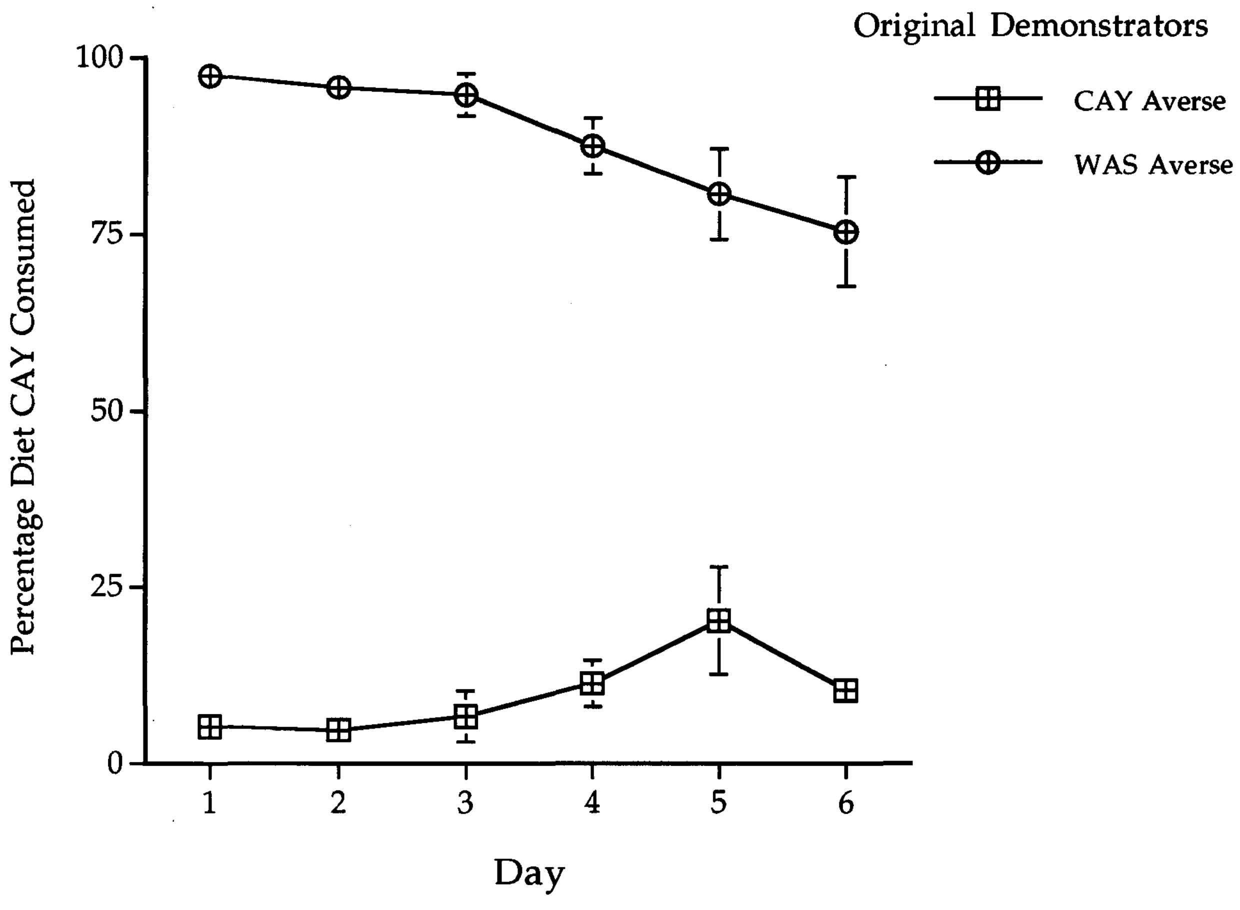


Figure 8: Random Placement Microculture
Post Floor Enclosure Test

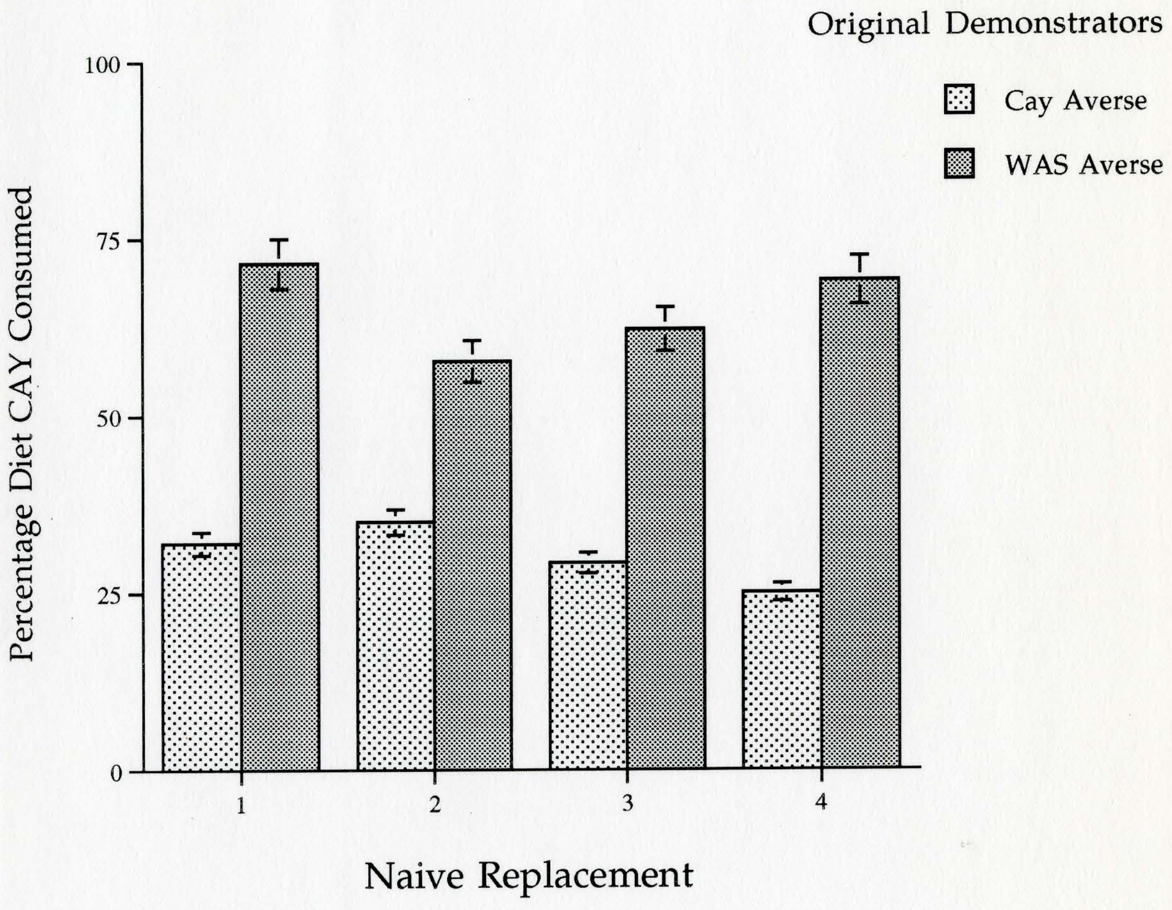


Figure 9: Observers Only Microculture

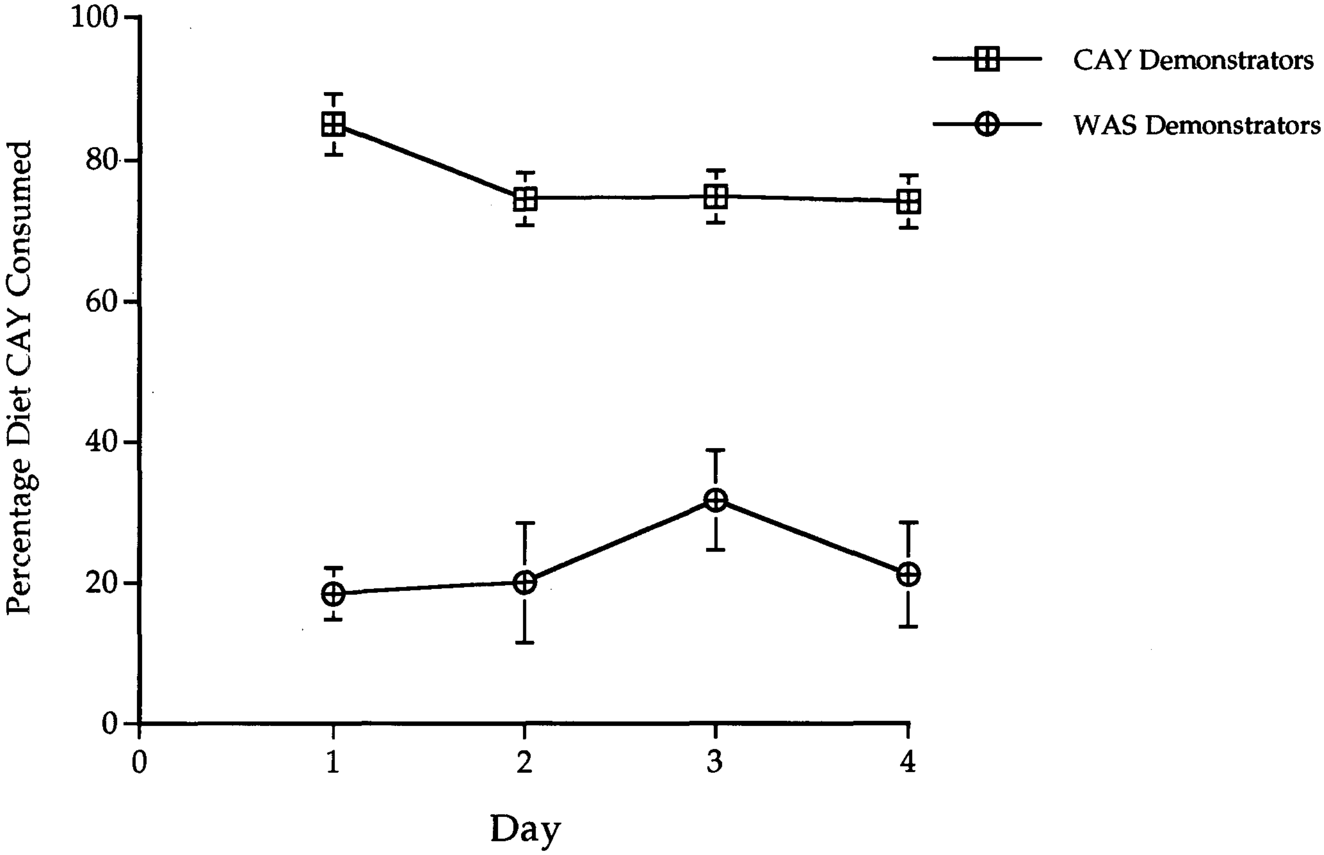


Figure 10: Observers Only
Post Floor Enclosure Test