

AN ABSTRACT FOR THE THESIS OF

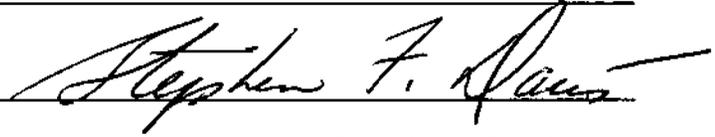
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SITUATION: TWO OBSERVERS RECEIVING DIFFERENT DIET MESSAGES

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For many years, scientists have asserted that social interaction plays a significant role in the transfer of information concerning food preferences. Posadas-Andrews and Roper (1983) identified two methods by which colonies of rats can obtain diet information: (1) directly, by ingesting the food itself, and/or (2) indirectly, by interacting with a conspecific, or animal of the same species. Recently, Galef and his colleagues (e.g., Galef, 1983; Galef, Kennett, & Wigmore, 1984; Galef & Wigmore, 1983) have repeatedly shown that a recently fed rat (a demonstrator) may transfer information regarding the type of food it has consumed to a naive animal (an observer). Such experiments typically have been conducted in

wire-mesh cages or a wooden maze. In conjunction with previous experiments conducted in our laboratory, the present study sought to extend the transfer of information paradigm to the open-field foraging situation. Thus, rather than having only two food sites to choose from, the animals would be confronted with six food sites. It has been shown in our laboratory that following interaction with a demonstrator which had consumed a specific test diet, the observer, when exposed to the free foraging situation, successfully exhibits an enhanced preference for the diet of its demonstrator partner. Additionally, studies conducted in our laboratory have found the same to be true when two observers receiving the same diet message were simultaneously tested in the foraging situation. The purpose of the present study was to expand these findings further. More specifically, two observers each provided with a different food-type message were tested. Positive results were obtained in the present study which mirrored the previous free foraging situation findings. Moreover, it could be concluded that the demonstrator is a viable source of diet information, and that animal-animal interactions which occurred between the two observers were not powerful enough to overthrow the two demonstrators original messages.

TRANSFER OF INFORMATION EFFECT
IN THE FREE-FORAGING SITUATION:
TWO OBSERVERS RECEIVING DIFFERENT DIET MESSAGES

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CHAPTER 1

INTRODUCTION

Social interaction plays an important role in the transfer of information concerning food preferences in many species. As humans, we are cognizant of the biological factors, such as gustatory and olfactory cues, involved in food selection, and we can identify environmental factors (e.g., cultural differences) that influence our diet selection. It has been observed that within a species, animals will seek out foods for ingestion that are similar. Young (1968), in an attempt to explain the incompatible results of food preferences in animals, concluded that a combination of sensory stimulations caused an animal to acquire certain food preferences. Additionally, he stressed the importance of hedonic processes and how they interact with the sensory components. Young focused on the biological aspects of preferred foods. The scope of contemporary research focuses more on the social or environmental influences. For example, Galef (1977) asserted that one must not neglect the social context in which feeding behavior occurs, as well as the biological factors involved in food preferences. Two methods utilized by colonies of rats to obtain diet information have been identified (Posadas-Andrews & Roper, 1983). First, rats

can obtain information by directly ingesting the food, or second, they can receive information indirectly by interacting with a conspecific, or animal of the same species.

It is thought that social transmission of information can serve an adaptive function by informing animals in their natural environment about the available resources, while saving the animal time and reducing its risk (Galef, 1977). Several researchers (e.g., Galef, 1977; Galef, 1982; Strupp & Levitsky, 1984) have cited Steiniger, an ecologist working on rat extermination in the 1950's, as being an early investigator of the effects that social learning has on adaptive behavior. For example, Strupp and Levitsky (1984) cited Steiniger for introducing the concept of "bait shyness." He found that rats when given poison bait in a specific area were, at the onset, accepting of the bait. However, with extended exposure to the poison bait their acceptance of it substantially decreased. This decrease in acceptance was even more noticeable in their offspring. Another example noted in Steiniger's writing of how social transmission of information for food preferences exists among animals was cited by Galef (1977). This example involved members of select colonies of rats in Germany. These colonies were

observed engaging in such behaviors as stalking, killing, and eating sparrows, while other various colonies did not exhibit this eating behavior even though sparrows were present within their environment.

These earlier findings have encouraged researchers to explore the mechanisms by which the transfer of distinctive feeding behaviors occur. Galef and his colleagues (e.g., Galef, 1983; Galef, Kennett, & Wigmore, 1984; Galef & Wigmore, 1983) are the most recent researchers to investigate this area. Their basic procedure involves allowing a recently fed rat (a demonstrator) to interact with a naive conspecific (an observer). They have found that the observer can extract sufficient information from its demonstrator partner, to enable it to subsequently identify and consume the specific food eaten by the demonstrator. This transfer-of-information process is shown clearly by the observer's enhanced preference for the diet eaten by its respective demonstrator.

Strupp and Levitsky (1984) used a slight variation of this basic procedure to look at the effects of an demonstrator-observer pair that were housed together for a period of time. Separated only by a wire mesh partition, the observer gained information from the demonstrator about the two food choices on a continuous

basis. Subsequently, the observer was tested for food preference in the wire mesh cage with the demonstrator present. In that the observer consumed more of the diet than its demonstrator partner had consumed, the results showed that the presence of the demonstrator did affect the observer's food preference.

Because the demonstrator plays a crucial role in the transfer of food-related information, Galef, Kennett, and Wigmore (1984) reported a series of studies designed to determine the generalizability of this phenomenon under different demonstrator-observer conditions. They found that the transfer-of-information effect was displayed by the following: (1) first generation wild rats (Rattus norvegicus), as well as domesticated rats; (2) food-deprived and nondeprived observers; (3) familiar and unfamiliar pairs of demonstrators and observers; (4) observers selecting fluids or solids; and (5) juvenile, as well as adult rats. Galef and Kennett (1985) reported data indicating that the cues emitted by the demonstrators are effective for up to 4hr after the ingestion of the diet.

Upon establishing the basic premise that a demonstrator rat can indeed transmit food related cues to a conspecific, the next obvious step was to ascertain the underlying mechanisms involved in this phenomenon.

Galef, Kennett and Stein (1985) stated that the first delineation to be made in considering such mechanisms should be a determination of the role of the demonstrator. For example, it might be argued that the presence of the demonstrator simply aids the observer in becoming familiar with the novel diet, thus reducing the observer's possible neophobic response to that diet. Neophobia, as described by Domjan (1977), suggests that rats tend to eat less of a novel substance than of a more familiar substance. Support for this argument was demonstrated by Posadas-Andrews and Roper (1983) when they found that simple preexposure to a novel diet enhanced the observer's preference for that diet. Hence, simple familiarity resulting in a reduction of neophobia may be an underlying mechanism.

Galef et al. (1985) sought to evaluate the underlying mechanisms that are induced by the demonstrator. Their procedure involved preexposing the observer animal to the two test diets, thus making both diets familiar on the test day. If simple familiarity with the test diet is a crucial factor, one might surmise that the subsequent demonstrator-observer interaction would have no effect on the observer's food preference. On the contrary, the results showed that the observer's diet selection was influenced by the

interaction with the demonstrator. It was concluded that the demonstrator does provide some type of contextual cue(s), which enable the observer to gain pertinent diet information. Additional supportive evidence for this conclusion also was reported by Galef et al. (1985). For example, an animal that has been anesthetized following consumption of the test diet is equally successful at transmitting the diet message as an alert animal. On the other hand, a surrogate "rat", constructed of cotton batting wrapped in surgical gauze and rolled in a specific test diet, does not influence the diet preference of the observer animal. Hence, simple preexposure to the test diet is not sufficient to produce the diet-preference effect in observers, rather, the mechanisms involved are directly related to demonstrator influence (Galef, Kennett, & Stein, 1985).

Having established the importance of the demonstrators per se, the next research issue dealt with the specific nature of the cues involved. What are the cues emitted by the demonstrator that cause its paired observer to prefer the designated diet? The most obvious candidates would appear to be those associated with the olfactory and/or gustatory modalities. Posadas-Andrews and Roper (1983) observed the contact between animals after the demonstrator had been given

access to a specific diet. They found that upon placing the animal back into the common cage, it was subjected to a thorough examination, such as sniffing, grooming, pawing, and licking, especially in the facial region. Observing this behavior lead them to suspect that the observer engages in these behaviors in order to gain information concerning the diet the animal had eaten. Hence, Posadas-Andrews and Roper (1983) identified several possible ways that food cues could be transmitted. First, particles of food that adhered to the demonstrator's face and paws could provide sufficient information. Second, they speculated that food odors could be detected on the demonstrator's breath, or in its feces.

Galef and Stein (1985) investigated the importance of facial contact between the demonstrator and observer. More specifically, they attempted to ascertain the minimum amount of time required for a successful information exchange to occur. It was found that demonstrator-observer interactions as short as 2 min were sufficient. Having obtained this information, they observed demonstrator-observer 2 min interactions and recorded the animal-animal contacts. Much to their surprise, they found that the observers spent an average of only 21.6 sec in direct contact with the

demonstrator. The majority of the time was spent in contacts involving the lower body area, while only a brief period of time was spent investigating the head and/or mouth. They did find, however, after analyzing the data that there was a direct correlation between the observer's preference for the demonstrator's diet and the mouth/face contact between the two animals.

Further, it was shown that demonstrators which had been stomach loaded could successfully transmit information. In other words, food residing in the digestive tract can produce effective cues. These findings are in agreement with the earlier statement made by Posadas-Andrews and Roper (1983), that particles of food adhering to the demonstrator's face and paws and/or odors on its breath could be important contextual cues provided by the demonstrator.

Clearly, the transfer-of-information effect has been established as a viable form of social learning. Galef and his colleagues have presented an elegant series of experiments delineating not only the sensory cues, but also the contextual cues provided by the demonstrator which are involved in this phenomenon. The ultimate goal in testing this effect would be to take it into the natural environment and apply the laboratory findings to animals in the wild. Before this procedure

could actually be engaged in, several basic questions remained unanswered. One such question involves the mechanisms by which the animal stores incoming information. Under natural circumstances, an individual rat might receive several different diet messages from conspecifics before it actually has the opportunity to forage. If this is the case then one must consider the effect of the multiple messages received, the time delay between when the demonstrator receives the initial message and transmits it to the observer, and the time delay that exists from when the observer actually utilizes the information conveyed to it by the demonstrator(s).

Galef (1983) has identified several capabilities that the recipient of information must have in order to effectively process incoming information from several conspecifics. First, the rat must be able to acquire sufficient information from each of the successive foragers in order to identify each diet message. Second, the rat must be able to encode the information in separable units for each encounter. Third, the animal must be able to hold the information in storage until it is ready for retrieval.

In order to test the cognitive capabilities of the animals, an experiment was designed in which the

observer was exposed to a series of four demonstrators, each of which had been given a different diet message (Galef, 1983). Subsequently, the animals were tested by presenting them with two test diets, one of which was novel, and the second of which had previously been eaten by one of the four demonstrators. The results of this experiment showed that the observer was able to differentiate between the two test diets by selecting the diet that it had previously been exposed to via one of its four demonstrator partners. The next question asked by Galef (1983) concerned the duration of such memory storage. In a subsequent experiment, the observers were divided into five groups: 0-, 6-, 12-, 24-, or 48-hr delay following the demonstrator-observer interaction. Results showed that under the 0-, 6-, and 12-hour delay conditions, the observer still exhibited an enhanced preference for the diet of its paired demonstrator. In the 24- and 48-hr delay conditions, the animals showed no specific diet preference. Hence, an observer appears capable of storing and retrieving information for up to 12 hours.

Despite the information that has been gathered, there are additional issues involving the transfer-of-information effect that must be resolved. A previous set of experiments (Davis, Richard, & Burke,

1986; Richard, Harrell, Davis, Wurtz, & Burns, 1986) conducted in our laboratory sought to replicate and extend the original Galef studies. Other than testing observers for food preference in a three-choice wooden maze (Galef, 1983; Galef & Wigmore, 1983), it does not appear that this phenomenon has been evaluated in other than suspended wire cages in the laboratory. Hence, the purpose of our first experiment was to determine if appropriate food-choice behavior would be displayed in a more naturalistic environment, such as the free-foraging situation offering access to six food sources. The results of this experiment were in agreement with those of Galef and his colleagues. The finding that an observer placed in the open-field foraging laboratory will seek out the specified diet consumed by its demonstrator from amongst several food sources is impressive. However, rats are seldom afforded the opportunity to forage in isolation. Thus, we conducted a second experiment in which two observers were concurrently exposed to the foraging laboratory following interaction with the same demonstrator. It was our intent to explore the animal-animal interactions between the two observers and to determine if these interactions interfered with retention of the original diet message. The results of this experiment clearly

indicated that pairs of observers given the same diet information will seek out and consume the diet of their demonstrator partner. In addition to showing support for the transfer of information phenomenon, the data provided pertinent information about observer-observer behavior. By way of closed circuit television, interactive behaviors were identified and quantified. We found that both observers spent significantly more time in contact with the appropriate food patches and that their first major eating bout tended to occur on an appropriate diet patch. These data suggest that the message provided by the demonstrator is quite robust and capable of withstanding animal-animal interactions, especially those in which one or both members of the pair had previous contact with a non-demonstrator food patch. In view of these findings, one must question the effect that two observers would have on foraging behavior if each observer was given a different diet message. The present study is designed to specifically evaluate this issue.

CHAPTER 2

METHOD

Subjects

Forty, 90-day old male Holtzman rats served as subjects. The animals were maintained on ad lib food and water in individual wire-mesh cages, with the exception of the conditions mentioned below. The animals were randomly assigned to four groups ($n = 10$): Demonstrator 1 (DEM1), Observer 1 (OBS1), Demonstrator 2 (DEM2), and Observer 2 (OBS2). Subsequently, one subject from each group was randomly assigned to a permanent DEM1-OBS1-DEM2-OBS2 squad. In each of the ten squads, the DEM1-OBS1 pair received the Cinnamon condition (CIN), whereas the DEM2-OBS2 pair received the Cocoa condition (COC).

Apparatus

Demonstrator chambers. Demonstrators received experience with their assigned test diet in a 10 g, glass aquarium (25.00 cm wide, 45.00 cm long, 30.00 cm high). Four such chambers, two for the habituation of the two demonstrators, one for the cinnamon (CIN) test diet, and one for the cocoa (COC) test diet, were located in a room adjacent to the general animal colony. A 4.00 cm layer of San-I-Cel animal bedding material (Paxton Processing Co., Paxton, IL) comprised the floor

of each enclosure.

Interaction chambers. Because the groups consisted of both a CIN demonstrator-observer pair, and a COC demonstrator-observer pair, independent interaction chambers identical to the ones described above were utilized.

Foraging laboratory. A 8.23 m by 2.21 m room, as shown in Figure 1, served as the foraging laboratory. The floor of the foraging lab was covered with 300 lbs of San-i-cel, average depth of 2.00 cm, in order to provide a more naturalistic environment. Six foraging patches were situated on the floor of the foraging lab. Each patch consisted of a piece of pine lumber to which the bottom portion of a one-gallon, plastic milk carton had been stapled. Subjects were given access to food via plastic tumblers which were attached with velcro fasteners to the center of the milk carton. The food cups were then surrounded with clay kitty litter to provide support and avoid spillage.

Procedure

In order to provide some degree of generalizability, the diets developed by Galef and his colleagues (e.g., Galef, 1983; Galef, Kennett, & Wignore, 1984) were employed. Six days prior to diet-preference testing, the four animals in the

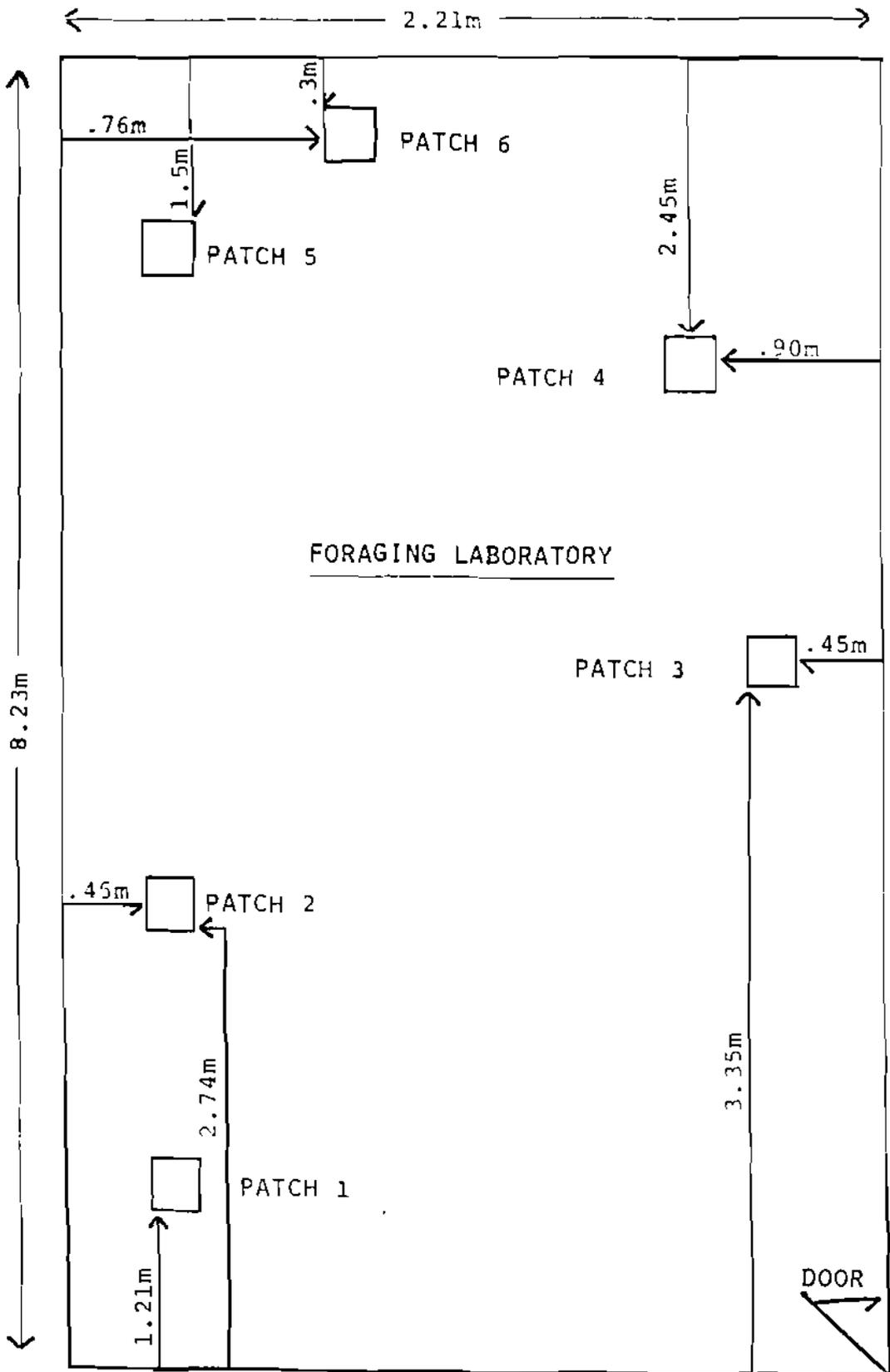


FIGURE 1: Diagram of the foraging laboratory. Three patches contained the cinnamon diet (CIN), and three patches contained the cocoa diet (COC) during diet-preference testing.

designated squad were placed on food deprivation for 24 hr. Subsequently, the DEM subjects received a 24-hr habituation session in the separate demonstrator chambers, which contained unadulterated, powdered Purina Laboratory Rodent Chow and a full water hottle. During this time, the OBS animals received a 24-hr habituation session in the foraging laboratory with powdered Purina Laboratory Rodent Chow available at each patch. Water was available in the foraging lab, via four 50-ml centrifuge tubes. Upon completion of the habituation session, the DEM animals and OBS animals were placed together in a double-size suspended cage (42.5 cm x 24 cm x 17.5 cm; Wahmann Co., Baltimore, MD) in the vivarium with food and water freely available. Twenty-four hr prior to diet preference testing all animals were again placed on food deprivation. Twenty-three hr later, the DEM animals were transported to separate test rooms and allowed 30-min access to the specified test diets, one received CIN, while the other received COC. The CIN diet consisted of powdered Purina Laboratory Rodent Chow into which 1%, by weight, McCormick's ground cinnamon was blended. The COC diet consisted of 2%, by weight, Hershey's pure cocoa blended into the powdered Purina Laboratory Rodent Chow. Following exposure of the DEM animals to their

appropriate test diets, they were placed with their respective observers, in the interaction chambers for 30 minutes. The OBS animals were then taken directly to the foraging laboratory for a two hour preference test session.

During diet-preference sessions, three foraging patches contained the CIN diet (40-60 g each), while the remaining three patches contained the COC diet (40-60 g each). The initial determination of the three CIN and three COC patches was random, but remained in effect for the testing of all OBS pairs. Water was available throughout the testing session. The order for testing the four-animal sub-groups was randomly determined.

CHAPTER 3

RESULTS

An analysis of variance (see Kirk, 1982) incorporating one between subjects factor (Type of Demonstrator: CIN versus COC) and one within subjects factor (Type of Diet: CIN versus COC) was performed on the mean food consumption scores. Likewise, an analysis of variance was performed on the mean time-of-patch-contact scores, which considered the main effects of Type of Observer (CIN versus COC) and Type of Diet (CIN versus COC). Simple main effects analyses were used to probe significant interaction effects. In order to compare the first major eating bouts of the CIN and COC observers, a chi-square analysis was employed.

Following the completion of each preference test session, the amount of food consumed (g) was determined for each patch. The three CIN and three COC scores were then added together to yield a single CIN consumption score and a single COC consumption score for each OBS pair. It was expected that the pairs of observers would preferentially consume a different diet, thus, comparable CIN and COC consumption scores would be predicted. Analysis of variance supported this prediction, $F(1, 8) = 1.09$, n.s.

The behavior of each observer pair was viewed on

closed circuit television during the two hour preference test. The following behaviors were recorded for each OBS animal: (1) patch contact scores (specific patch contacted and the duration of the contact), and (2) interaction scores (the amount of time spent in physical contact between the two OBS animals). Each member of the OBS pair was independently viewed by a separate experimenter with the assignment of the specific OBS animal being random at the start of each test session.

Mean time-of-patch-contact scores for the first 20 patches contacted were analyzed, and the results are shown in Figure 2. Analysis of variance of these scores yielded significance for the Type of Observer x Type of Diet interaction, $F(1, 18) = 7.531$, $p = .012$. Simple main effects analyses employed to probe this interaction indicated that the CIN observers spent significantly more time, $F(1, 36) = 4.86$, $p < .05$, contacting cinnamon patches, while COC observers spent significantly more time, $F(1, 36) = 4.18$, $p < .05$, contacting cocoa patches. Additionally, the occurrence of the first major eating bout, defined as a patch contact of 30 sec duration or longer, for both the CIN and COC observers were considered. For the CIN observers, 8 of 10 such feeding bouts occurred at cinnamon patches, while 9 of 10 such bouts occurred at cocoa patches for the COC

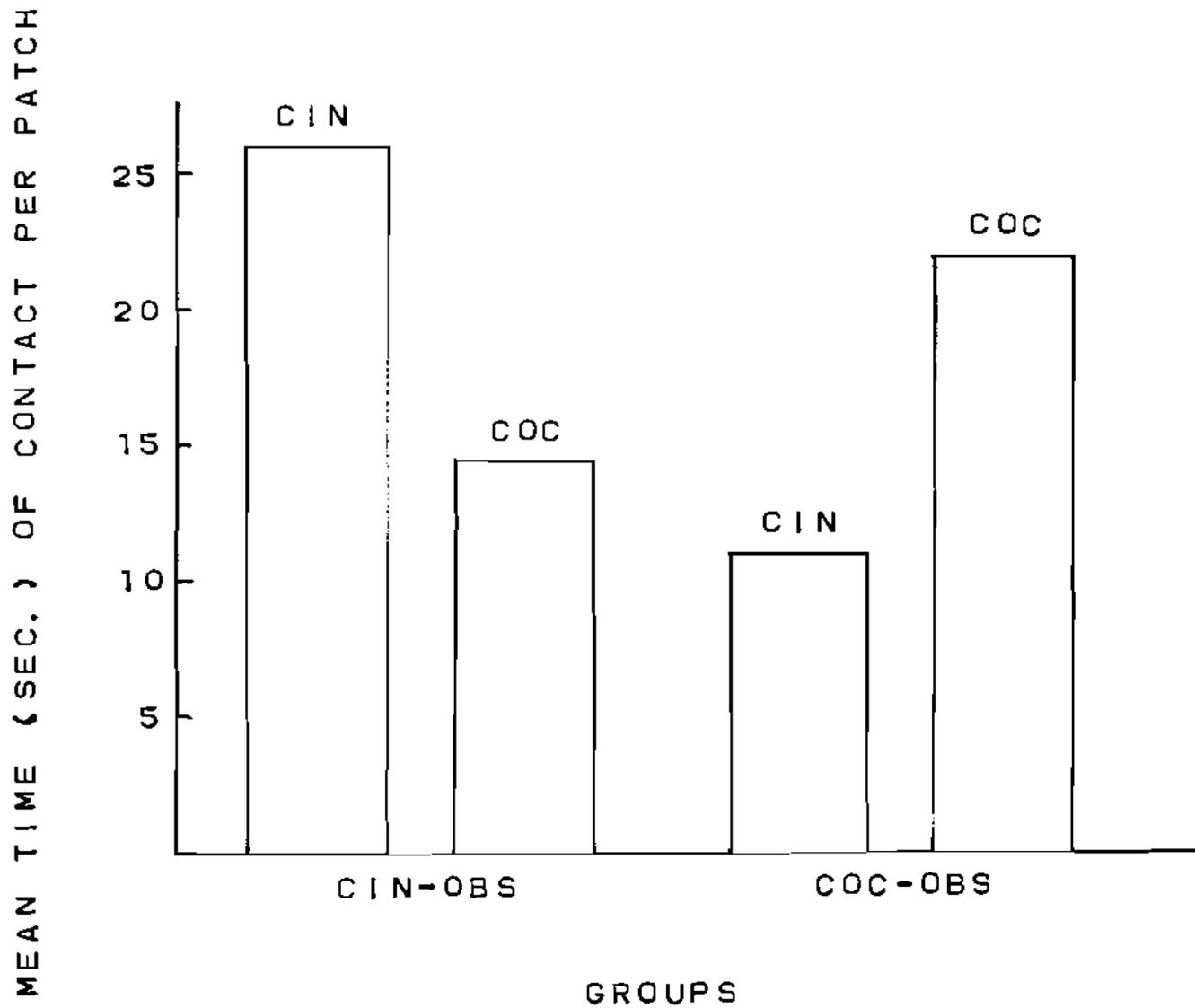


FIGURE 2: Mean time-of-patch-contact scores (seconds) as a function of Type of patch and Type of Observer.

observers, $\chi^2(1) = 7.27$, $p < .01$. Clearly, these results indicate that the message originally provided to each observer is quite pervasive and resistant to change by a variety of factors.

CHAPTER 4

DISCUSSION

To recapitulate, the purpose of the present study was to assess the extension of the transfer of information findings to the free foraging situation. More specifically, the present study sought to evaluate the animal-animal interactions and the effect of these interactions when considering the presence of two observers that had been given different diet messages.

This experiment extends the initial work of Galef and his colleagues (e.g., Galef, 1983; Galef, Kennett, & Wigmore, 1984; Galef, & Stein, 1985; Galef & Wigmore, 1983) in several important ways. First, it demonstrates that the transfer of information phenomenon can be generalized to the open-field foraging situation. This generalization is quite impressive when one considers the fact that the animals were confronted by six eating sites to choose from, compared to only two containers employed in the previous studies. Additionally, the present data support a second generalization. As the previous studies reported by Galef and his colleagues have employed hooded rats as subjects, the present experiment involved the use of albino rats, clearly supported the generalization of this behavior to a second strain of rats.

The robustness of this phenomenon is displayed further when one considers the dependent variable measures presented in this study which were the time-of-patch-contact scores, and the occurrence of the first major eating bout. It has been established in a previous experiment (Davis, Richard, & Burke, 1986) involving the foraging laboratory that a message simultaneously transmitted by a single demonstrator to two observers can endure direct contacts with the second observer. The present experiment extended those results by showing that two observers independently provided different food-type messages prior to a joint foraging session chose those patches containing the diet that corresponded to that of their respective demonstrator partner.

Given these results, one might conclude that some rather dramatic event must occur to modify the demonstrator's message once it has been processed by the observer. Thus, the interaction of observers that had just consumed an alternate food is insufficient to alter the message. The lack of effective observer-observer communication suggests that animals may need to have food-stuff present in the digestive system for a certain period of time for the transmission of diet-preference information to be successful. Sufficient time in the

digestive tract may not have elapsed in the present study for the non-demonstrator foods to become effective cues for transmission. It will be recalled that Galef and Stein (1985) reported positive effects when the mouth of the demonstrator was contacted, when the stomach was loaded, and when a rat (not a surrogate) was employed to transmit the cues. These data would appear to be supportive of the type of mechanism proposed here.

As stated, the results of the present study extend the transfer of information phenomenon to the free-foraging situation. Additionally, the results reiterate the importance of the demonstrator by indicating that animal-animal contacts between the two observers with different diet messages have no effect on the original demonstrator message. Thus, the mean time-of-patch-contact scores and the occurrence of the first major eating bouts were in accordance with the appropriate type of demonstrator and type of patch contact. However, the picture is still unclear concerning rodent foraging behavior. When given multiple diet messages, with all of the specific foods accessible for consumption, which diet message would the animal attend to? Hence, in this situation one might successively expose a single observer to a CIM demonstrator and then to a COC demonstrator (and vice

versa) and then record the observer's diet preference. Such an experiment would address the importance of primacy versus recency of demonstrator's message to the observer. Another possible research issue would be to explore the direct transfer of information concerning a food aversion, rather than a preference. These research topics have been briefly addressed in the literature. However, additional studies are warranted to provide a greater understanding of the mechanisms involved in the transmission of diet information.

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