

**PREFERENCE FOR A HETEROSPECIFIC
DEMONSTRATOR IN A TERRITORIAL DOVE**

By

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A thesis submitted to the faculty of Graduate Studies and Research
in partial fulfillment of the requirements for the degree of Master
of Science.

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March 1991

Abstract

This thesis examines the hypothesis that social learning in the territorial Zenaida dove (*Zenaida aurita*) functions primarily in a mixed species foraging context. The study was composed of two parts, a field study and a laboratory study. The field study recorded foraging associations and interactions between Zenaida doves and the other species with which they commonly aggregate, focusing on joining behaviour and aggression. The Carib grackle (*Quiscalus lugubris*) was the most frequent foraging associate of Zenaida doves. Zenaida doves tended to join other foragers on the basis of the number of birds present, irrespective of species, but were selectively aggressive towards conspecifics. This resulted in Zenaida doves foraging most often alone or in the company of grackles. Grackles, therefore, appear to be the most stable potential source of social information for foraging Zenaida doves.

The laboratory study consisted of two experiments where conflicting information about a novel food type and a novel food-finding problem was provided simultaneously by a conspecific and a heterospecific (grackle) demonstrator. Both experiments showed that not only could Zenaida doves learn from another species, but that they preferred the heterospecific demonstrator over the conspecific. This preference was so strong that Zenaida doves performed the irrelevant control behaviour shown by the grackle even when the correct information required to solve the novel food-finding problem was given to them by another dove. The results suggest that social information may be obtained more readily from foraging associations that involve scramble competition rather than interference competition and that the role of conspecifics may be overemphasized in cultural learning.

Résumé

Cette thèse examine l'hypothèse selon laquelle l'apprentissage social chez la tourterelle territoriale *Zenaida aurita* se produit principalement lorsque celle-ci cherche de la nourriture en présence d'individus d'une autre espèce. L'étude s'est effectuée en deux parties, la première sur le terrain et la seconde en laboratoire. Lors du travail de terrain, on prenait note des oiseaux qui mangeaient ensemble et de toutes les interactions entre eux, avec une attention particulière portée aux comportements d'agression et d'attraction intra- et interspécifique. Le mainate Caraïbe (*Quiscalus lugubris*) est l'espèce la plus fréquentée par les tourterelles lors de leur quête de nourriture. Les tourterelles semblent se joindre au hasard aux autres oiseaux, quelle que soit leur espèce, en fonction du nombre présent sur le site. L'aggression est presque exclusivement dirigée vers les congénères. La conséquence de ces deux phénomènes est que *Zenaida aurita* s'alimente le plus souvent seul ou en compagnie de mainates, et très rarement en compagnie de congénères. Le mainate Caraïbe est donc pour *Zenaida aurita* la principale source stable d'information alimentaire.

Le travail de laboratoire comportait deux expériences. Dans la première, une tourterelle naïve observait un congénère et un mainate qui mangeaient chacun un type nouveau de nourriture. Dans la seconde expérience, une nouvelle technique de recherche alimentaire était montrée soit par une tourterelle soit par un mainate. Les deux expériences ont démontré non seulement que les tourterelles peuvent imiter une autre espèce, mais qu'elles préfèrent copier un mainate plutôt qu'un congénère. Cette préférence est si forte que les tourterelles effectuent le comportement incorrect montré par un mainate même quand la solution appropriée au problème alimentaire est montrée par une autre tourterelle. Les résultats suggèrent que l'information sociale peut s'obtenir plus facilement dans des situations de compétition alimentaire à consommation rapide que dans des situations de compétition agressive. Ils portent aussi à penser que l'importance que l'on accorde traditionnellement au congénères dans l'apprentissage social est surfaite.

Acknowledgements

I would foremost like to thank my supervisor Louis Lefebvre for providing me with such an interesting project to work on and for all of his time and effort during the preparation of my thesis. I would also like to thank the members of my supervisory committee Luc-Alain Giraldeau, Wayne Hunte and Bob Lemon for their help with my thesis proposal and their attempts to understand my data analysis.

I owe the success of my field season and many thanks to Fred Goodfellow for being not only a biologist, but also a carpenter, a veterinarian, a car mechanic, and a great friend. I am especially grateful for his assistance during 5 am field trials, and never ending cage experiments and for his wonderful idea of using caged doves to attract and trap other doves.

I would also like to show my appreciation to Boris Palameta, Alastair Inman and Danny Weary, for all their help with my analysis and the writing of my thesis.

Last, but not least, I want to thank Trudi Collins, Toni Johnson, Chris Parker and Lotus Vermeer in Barbados, and Danielle Cantin, Lauren and Colin Chapman, Karen K. Hatch, Alastair and Ann Inman, Joyce Marsolais, Boris Palameta, Karen Richardson, and Lucie Robidoux in Montreal for making the three years of my M.Sc. such great ones. And I would like to especially thank Fred Fleisler for all of his moral support.

1. GENERAL INTRODUCTION

Cultural Transmission

Cultural transmission is the diffusion of novel behaviours through animal populations via social learning, the transfer of information from a knowledgeable demonstrator to a previously naïve observer (Bonner 1980). Novel behaviours can also spread through populations via two other means, individual learning and reproductive transmission of genotypic modifications. Compared to these two alternatives, cultural transmission is thought to be rapid and flexible (e.g. Galef 1976, Mainard 1980).

Social learning, the process by which behaviours are culturally transmitted, may take several forms according to the complexity of the information (Thorpe 1963). In the simplest of cases, the attention of the observer is attracted to the part of the environment the demonstrator is interacting with, a process known as "stimulus enhancement" or "local enhancement". For the new behaviour to be performed correctly by the observer, information must then be completed by individual learning. In more complex cases, the precise novel motor act performed by the demonstrator is copied by the observer, a process known as "imitation". Clear demonstrations of imitation are rare in the literature, since extensive experimental controls are necessary to exclude the simpler forms of social learning (Palameta and Lefebvre 1985, Lefebvre and Palameta 1988, Palameta 1989).

In addition to these two mechanisms, apparent cases of social learning may be caused by social facilitation and by natural shaping. In the first case, the behaviour is not new and is simply latent in the observer's repertoire; the performance of the behaviour by the demonstrator simply serves as a stimulus to elicit the same behaviour in the observer (Clayton 1978). In the case of natural shaping, the effect of the demonstrator is indirect: its performance of the new behaviour modifies the environment in a way that makes individual learning easier for other animals (Sherry and Galef 1984).

Examples of Cultural Transmission

Many cases of presumed cultural transmission have been reported in the wild, particularly for foraging behaviour (for reviews, see Galef 1976 and 1988, Mainard 1980, Bonner 1980, Lefebvre and Palameta 1988). Classic examples of these include milk bottle opening by British tits (*Paridae*) (Fisher

and Hinde 1949, Hinde and Fisher 1951), blood sucking by Galapagos finches (Bowman and Billeb 1965), washing sand from potatoes and wheat by Japanese macaques (Kawai 1965), hammering or stabbing open mussels by oystercatchers (Norton-Griffiths 1967 and 1969), termite fishing by chimpanzees (van Lawick-Goodall 1968), and diving for molluscs by Norway rats (Gandolfi and Parisi 1973, Parisi and Gandolfi 1974)

Milk bottle opening is thought to have originated independently in a few birds. The behaviour of piercing through the tops of milk bottles to feed on the cream quickly spread geographically and was thought to depend on stimulus enhancement of milk bottles as a novel food source (Fisher and Hinde 1949, Hinde and Fisher 1951)

The practice of sucking blood, both a novel food source and foraging technique for Galapagos finches, may have begun as a mutualistic relationship where the finches caught and ate insects parasitizing two species of birds of the genus *Sula*. Possibly through stimulus enhancement or natural shaping the finches began parasitizing the boobies themselves by piercing their skin in order to feed on their blood (Bowman and Billeb 1965)

In Japanese macaques, the origin of two novel foraging behaviours concerning familiar food items could be traced back to one juvenile female Imo. Imo first developed the habit of washing sand from potatoes by dipping them in the sea and then later discovered that she could separate wheat grains from sand by throwing it into the water as the wheat floated and the sand did not. Both behaviours slowly spread to the majority of the troop through social learning (Kawai 1965)

When first studied, oystercatchers feeding on mussels were found to use two foraging techniques, hammering or stabbing. Each individual used only one of the two methods and mated birds were found to use the same technique. Offspring used the same technique as their parents. In comparing offspring feeding on mussels to offspring feeding on worms, it was found that the former took much longer to fledge. This was thought to confirm that offspring were learning the foraging techniques from their parents, as foraging on mussels requires more skill than foraging on worms (Norton-Griffiths 1967 and 1969)

Chimpanzee offspring were also thought to learn a new foraging technique, fishing for termites, from their parents through social learning. This idea was supported by observations of young chimpanzees using

inappropriate twigs and fishing techniques which resulted in failed attempts to feed on termites. Whenever adults displayed tool-use, the young chimpanzees watched closely and often played with the tools as soon as the adults discarded them (van Lawick-Goodall 1968).

In the case of wild rats, preliminary field observations suggested that novel foraging techniques as well as novel food sources were being culturally transmitted. Different rat colonies studied along the banks of the Po River in Northern Italy were found to vary both in their preferred prey species and harvesting method. While members of some colonies of wild rats dove underwater for molluscs, members of other colonies waited for low tide to dig them out of the river bottom (Gandolfi and Parisi 1973, Parisi and Gandolfi 1974).

Problems in the Literature

The main problem with this literature is that many of the reported instances of cultural transmission are anecdotal. It is thus difficult to see if all cases are truly cultural or if some of them represent other forms of transmission. Even if they are cultural, the precise nature of the information transmitted is difficult to determine in the absence of controlled experiments. These problems have led, among others, Galef and his colleagues (Galef 1976, Galef 1980, Sherry and Galef 1984 and 1990, Galef 1988) to seriously question the apparent widespread occurrence of cultural transmission. Controlled experiments have shown that many of the cases of presumed cultural transmission described above can be explained by simpler mechanisms.

Galef (1980) brought the diving behaviour of wild rats (Gandolfi and Parisi 1973, Parisi and Gandolfi 1974) into the laboratory to determine the extent social learning played in the development of this foraging behaviour. Using chocolate as the food source, it was found that naive adults did not learn to dive as a result of interactions with a diving conspecific, but could learn through natural shaping by gradually increasing the water depth covering the food. It was also found that learning to swim can easily lead independently to diving, however social interaction was not necessary for the spread of swimming. Therefore, the behaviour of diving for food could have spread through the wild colonies through a combination of natural shaping by the

environment and individual learning and did not necessarily involve social learning.

The behaviour of opening milk bottles by British tits (Fisher and Hinde 1949, Hinde and Fisher 1951) was brought into the laboratory by Sherry and Galef (1984, 1990). Wild chickadees, the North American equivalent of British tits, were caught and tested with small foil-covered plastic tubs full of cream. The results of these studies show that more chickadees learn the behaviour of milk bottle opening when allowed to interact with an opened tub or with a closed tub in the presence of a conspecific. It was suggested that the presence of a conspecific may have reduced the observer's fear or vigilance or may have elicited foraging, all of which could have facilitated food discovery. The results, therefore, provide no evidence that imitation was required for the spread of this behaviour. Milk bottle opening probably spread due to a combination of birds independently initiating the behaviour and birds learning the behaviour from other birds, either directly through local enhancement or indirectly through interaction with opened milk bottles, i.e. natural shaping.

A long-term experimental field and laboratory study on oystercatchers by Goss-Custard and colleagues has worked towards a better understanding of oystercatcher's foraging behaviours on mussels. It is now known that oystercatchers regularly switch from one specialized feeding technique to another (Goss-Custard and Sutherland 1984) and that prey choice and foraging behaviours vary with age (Goss-Custard and Durell 1983). Following these discoveries, culture is no longer believed to be the explanation behind the development of foraging techniques in oystercatcher offspring.

Recently, Visalberghi and Fragaszy (1990b) brought the behaviour of food-washing into the laboratory to study it more closely in tufted capuchin monkeys and crab-eating macaques. Food-washing has been one of the most widely cited examples of cultural behaviour in monkeys, but the original observations did not include the sequence of events preceding the innovation of this behaviour (Itani 1958, Kawai 1965). When all behaviours leading up to food washing were recorded under controlled conditions, it was found that food-washing was most likely to occur when an individual showed a lot of interest in both sandy fruit and the water. No evidence of imitation was found by Visalberghi and Fragaszy (1990b). It is therefore possible that Japanese macaques learned to wash individually with the aid of some natural shaping and social facilitation.

Although many presumed cases of cultural transmission are thus open to question, the presence of imitation has at least been strongly demonstrated in feral pigeons (*Columba livia*) in a series of studies by Palameta and Lefebvre. In the field, Lefebvre (1986) has shown that a novel food-searching technique, piercing the paper cover of a box containing feed, can spread through urban populations of feral pigeons. In the laboratory, Palameta and Lefebvre (1985) and Lefebvre and Palameta (1988) have shown that observers respond to the amount of information available from demonstrators when learning the paper-piercing technique. Information of the type given by social facilitation or natural shaping leads to little or no learning; observers given complete demonstrations of both piercing and eating by the demonstrator are the ones that learn the most rapidly, while observers given incomplete information learn at a slower rate. In a series of experiments that rules out any other mechanism except imitation of the precise novel motor act of the demonstrator, Palameta (1989) has further pinpointed the information that pigeons are capable of using in cultural transmission. Observers were shown to use precise variations in the demonstrator's food-searching technique when all apparatus-related cues were rigorously controlled, thus eliminating any possible stimulus or local enhancement.

The Evolution of Cultural Transmission

Presumed instances of cultural transmission thus require extensive laboratory experiments to pinpoint the mechanisms thought to be operating. Laboratory investigations of social learning have been numerous (see Galef 1988 for a review), but have often involved arbitrary skills which would not normally be required by the animal in the field. Pigeons have for instance been required to push ping-pong balls (Epstein 1984) or peck at disks (Bullock and Neuringer 1977, Skinner 1962), cats (Chesler 1969, John et al. 1968) and rats (Corson 1967, Gardner and Engel 1971, Jacoby and Dawson 1969) to press a lever, and puppies to pull a cart (Adler & Adler 1977).

The combination of anecdotal reports from the field and of arbitrary laboratory experiments has thus led to a divorce between studies conducted in the field and in captivity. To a certain extent, this divorce may have prevented our understanding of the conditions that have favoured the appearance of cultural transmission in animals. The only empirical attempts to understand these conditions have been the studies of Klopfer (1959 and 1961) and

Sasvári (1979 and 1985) on opportunism and those of Lefebvre and Palameta on group-living (Lefebvre and Palameta 1988 and MS).

In Klopfer's studies, a series of experiments were designed to analyze the role of cultural transmission in the origin of species-specific behaviours. Two species were compared: greenfinches (*Carduelis chloris*) and Great tits (*Parus major*), on a task that involved discriminating between whole sunflower seeds and sunflower seeds filled with aspirin, placed on different backgrounds. It was suggested that an opportunistic species (Great tits) would be more likely to learn about novel foods through observation than a conservative or specialist feeder (greenfinches). In a preliminary study (Klopfer 1959), greenfinches were tested under three different conditions: alone, with a knowledgeable partner or with a naive partner. The birds learned equally well in the first two groups but did not learn in the last group. In the second study (Klopfer 1961), greenfinches and Great tits were tested alone or with a naive partner. Greenfinches in pairs required a longer time to learn than did single birds. Very few Great tits failed to approach the food, and both paired and single birds learned the discrimination equally well.

Turner (1964) has criticized these experiments for being "unnatural" and too difficult, because they require microhabitat discrimination. Greenfinches have since been observed to use feeding conspecifics as indicators of good foraging sites, a form of social learning involving local enhancement (Newton 1973).

Sasvári (1979 and 1985) compared species that differed in their adaptability in urban environments. He looked at three *Parus* species: Great tits (*Parus major*), Marsh tits (*Parus caeruleus*) and Blue tits (*Parus palustris*), and two *Turdus* species: blackbirds (*Turdus merula*) and songthrushes (*Turdus philomelos*). For the *Parus* species, the task involved lifting a piece of linen hanging vertically to obtain food behind it. For the *Turdus* species, the task involved pulling a string out of a test tube with food attached to the end. The most successful species were the Great tits and the blackbirds. Both of these species inhabit urban environments, whereas the others do not. In both the experiments by Klopfer (1959 and 1961) and by Sasvári (1979 and 1985), the observer and demonstrator were never separated, and thus the observer could obtain food by parasitizing it from the demonstrator. This may have interfered with social learning, since Giraudeau and Lefebvre (1987) have

shown that intraspecific parasitism or "scrounging" may inhibit cultural transmission.

More importantly, neither Klopfer nor Sasvári systematically controlled for factors extraneous to their hypothesis when comparing different species. If one species responds differently to caging, testing and/or handling by humans or the features used in the experiment (stimuli, motor task, reward) then differences in the outcome of the experiments may be due to these factors and not to the precise hypothesis being tested. This is particularly true of Sasvári's experiments, where adaptation to urban living may be thought to require a greater tolerance to the close proximity of humans and thus bias the laboratory study a priori in favour of urbanized species.

The study by Lefebvre and Palameta (MS) incorporated such controls in their test of the role of gregariousness in the evolution of social learning. They compared a group-living species, the Feral pigeon (*Columba livia*) to a solitary species that defends year-round territories, the Zenaida dove (*Zenaida aurita*) (Lefebvre, MS). Zenaida doves are a good choice for a comparative study with pigeons as both species are opportunistic, urbanized columbids that exploit human-provisioned foods (Bond 1971, Haverschmidt 1969). Extraneous factors were controlled either by comparing the species on two forms of learning, social and individual, or by making sure the species did not differ a priori by shaping them to identical levels of proficiency on the basic steps required to solve the feeding problem. The results clearly showed that group-living is not essential for social learning as Zenaida doves were capable of imitating a conspecific.

These findings pose an interesting question: if a territorial dove is capable of imitation, when does it use this ability and how did the ability evolve? One possibility is that imitation is a vestigial character that evolved in some ancestral gregarious columbid. This possibility is untestable, however, since it is based on a phyletic argument. A second possibility is that imitation is used within the kin unit, i.e. between mates and offspring, which overlap and tolerate each other on one territory. This possibility is difficult to test in the field, since it requires the identification, observation, capture and testing of a large number of kin groups. A third possibility is that the ability to imitate in a territorial animal such as the Zenaida dove is used primarily in mixed species groups. This is the hypothesis that will be tested in this thesis.

Cultural Transmission in Mixed Species Groups

Like many other territorial birds, Zenaida doves are intolerant to conspecifics but often forage in association with other species. Mixed species groups of Zenaida doves and Carib grackles (*Quiscalus lugubris*), Lesser Antillean bullfinches (*Loxigilla noctis*), Common Ground doves (*Columbina passerina*) and Glossy cowbirds (*Molothrus bonariensis*) are often seen in Barbados (pers. obs). Since these mixed species groups appear to involve low levels of aggression and high levels of foraging association, it is possible that this is the context in which imitation is used by the Zenaida dove.

The use of imitation in mixed species groups implies that social learning occurs between species. The examples given earlier all involved cultural transmission within species, which is by far the most widely studied form of social learning. Cultural transmission between species has nevertheless been reported in a number of cases. For one, the classic case of birds opening milk bottles has been reported to occur between species as well as within (Fisher & Hinde 1949).

Examples of Interspecific Cultural Transmission: Field Studies

Field studies have provided several other examples of social learning between heterospecifics. The most common information to be learned appears to be the location of clumped food patches, presumably through local enhancement. This was observed in mixed species flocks of insectivorous tropical birds (Macdonald & Henderson 1977) and in mixed species finch flocks (Rubenstein et al. 1977) where there were species-specific roles and little or no aggressive interactions. In both these studies, feeding with heterospecific neighbors was found to significantly increase the duration of a feeding episode, complete dietary overlap was also observed.

Caldwell (1981) found mixed species heron flocks to be attracted to a foraging site by the presence of Snowy egrets. In addition, there was an increase in the herons' foraging success when in the proximity of the Snowy egrets. Nine species of ciconiiforms (storks, ibis, spoonbill, herons, and egrets) were also found to be attracted to a feeding site by white and blue wire and paper models, but the birds only remained at a site when feeding success was high (Kushlan 1977).

In the study by Williamson and Grey (1975), starlings foraging in mixed species flocks were found to modify their foraging behaviour to resemble the

other species with which they were foraging. Sunbirds copied both where and how white-eyes foraged whenever this species was present (Greig-Smith 1977). In mixed flocks of flycatchers and kinglets, individuals were found to learn to recognize and avoid noxious foods from one another (Cook et al. 1969).

House finches appeared to learn a novel food source and feeding technique from hummingbirds. These finches normally fed on the fruit of a fig tree, but when the tree's food supply became exhausted, the finches began imitating the hummingbirds by hovering to feed at an artificial nectar feeder. While the finches were noted to be aggressive to all other species, no aggression towards hummingbirds was recorded (Taylor 1972). In a similar example, robins were found to copy the foraging techniques and food choice of Cedar waxwings. When foraging together, robins imitated the waxwings by hovering to feed on juniper berries (Maclean 1970).

Examples of Interspecific Cultural Transmission: Laboratory Studies

In the laboratory, many different species have been paired for studies of interspecific social learning of foraging behaviours. Studying mixed flocks of chickadees, Krebs (1973) found an increase in feeding success relative to homospecific flocks, which he attributed to social learning. The birds were observed to alter their searching pattern whenever an individual of another species determined the contents of a certain patch. This study suggested that the total scanning range of a mixed species flock could be increased by combining the separate searching skills of different species.

In his study on different *Parus* and *Turdus* species, Sasvári (1985) compared the learning abilities of both adults and juveniles, when paired with a conspecific and a heterospecific demonstrator. It was found that adults learned more easily from a conspecific while juveniles learned equally well from both. Turner (1964) found that sparrows were more likely to eat a novel food after observing a chaffinch eating it. However, more sparrows responded to a conspecific eating a novel food than to a chaffinch.

In rodents, Mainardi et al. (1972) showed that Golden hamsters can learn to obtain food dangling from a chain by observing. House mice demonstrate the technique. A study on male Albino rats produced no difference in learning a task, when comparing a group observing a Mongolian gerbil demonstrator and the control group learning from a conspecific (Benel 1975).

Millikan and Bowman (1967) describe interspecific social learning of tool use. Although never reported to use tools in the wild, one species of Galápagos finch was found to manipulate sticks to pry food items out of narrow cracks after being caged with a tool-using finch of another species. An anecdotal report of food avoidance was given by Rothschild and Ford (1968), where a hand reared starling observed the reaction of a hand reared thrush to a poisonous grasshopper. When itself presented with a similar grasshopper, the starling ignored it and imitated the thrush's reaction of beak wiping.

Social learning has also been observed in reptiles, as seen in the case of the Blue Spiny lizard, a carnivore, which ate lettuce for the first time after observing a herbivorous species, the Desert Iguana eat it. In these animals, food stealing is common and is thought to be a source of information about novel prey (Greenberg 1976).

Mammals in captivity have also been found to imitate other species. A female Bottlenose dolphin imitated the sleep postures, comfort behaviours and swimming postures of a male Cape fur seal. A male dolphin imitated the cleaning behaviour of a scuba diver and the sound of his regulator. These behaviours were performed in the absence of the demonstrators (Tyler and Saayman 1973).

Problems in the Literature

If one wishes both to understand the precise nature of the information being transmitted and to work within an ecologically relevant context, the literature on interspecific cultural transmission suffers from the same problem as the one mentioned earlier for learning within species: a divorce between field reports and laboratory experiments. Not only are some of the tasks used in the laboratory very different from the behaviours reported to be culturally transmitted in the field, but pairing of demonstrator and observer species is also often arbitrary, frequently involving species that do not co-occur in the field. For example, in the study by Millikan and Bowman (1967), the two species of Galápagos finches used (*Geospiza conirostris* and *Cactospiza pallida*) inhabit different islands (Butler 1979). The Blue Spiny lizard (*Sceloporus cyanogenys*) and the Desert Iguana (*Dipsosaurus dorsalis*) in the study by Greenberg (1976) are found in different parts of the southwestern United States without overlap (Cohran & Groin 1970).

Thesis Goals

The goal of this thesis is to demonstrate that Zenaida doves are capable of interspecific social learning and that this capacity functions in the context of mixed species foraging aggregations. The study will attempt to avoid some of the problems mentioned above by integrating field and laboratory data and designing ecologically-relevant experiments based on prior observations of natural foraging associations.

The thesis is composed of two parts. The first part consists of a field study in which foraging associations between Zenaida doves, Carib grackles, Ground doves, Glossy cowbirds and Lesser Antillean bulfinches are systematically recorded. These data will be used to determine the potential for social learning to occur, either intra- or interspecifically. Foraging interactions will also be recorded to determine if Zenaida doves preferentially forage with one species or another. The field trials are conducted at different sites on the west coast of Barbados and include both trials with provisioned food and trials without provisioning. The former are designed to study foraging associations in a context that increases animal numbers and the frequency of foraging interactions. The latter set of unprovisioned trials is a control for the potentially unrealistic effects of increased food and animal numbers.

The second part is an experimental laboratory study consisting of two experiments performed on wild-caught birds. The first one features a novel food similar to the one used in the provisioned field trials, the other features a novel food-finding problem, i.e. removal of an obstacle with the beak, a common foraging technique in Zenaida doves. In both cases, Zenaida doves are given conflicting information by a conspecific and a heterospecific demonstrator. The heterospecific demonstrator is chosen from the species found to be the most frequent foraging associate of Zenaida doves in the field study. These experiments are the first to look at demonstrator preference by requiring an observer to make a choice between a conspecific and a heterospecific that provide simultaneous but contradictory information.

If social learning in a territorial animal functions primarily in the context of mixed species groups, Zenaida doves should learn selectively from the heterospecific model. If this occurs, it would be the first case of interspecific social learning where a heterospecific demonstrator is preferred over a conspecific.

2. PART A - FIELD STUDY

Introduction

Advantages of Group Foraging

Group foraging in birds is a well studied phenomenon (see reviews by Pulliam and Millikan 1982, Barnard and Thomson 1985, Clark and Mangel 1986). Two main advantages have been proposed as the functional basis for its occurrence: 1- decreased predation risk and 2- increased feeding efficiency. Empirical evidence that foraging in groups reduces risk of predation in wood-pigeons was provided independently by Siegfried and Underhill (1975) and Kenward (1978). It has been found, both in House sparrows (Elgar 1986) and in Black-capped chickadees (Ficken 1981) that solitary birds established foraging flocks by calling whenever their food find was easily divisible, which also suggests that reduced predation may be one advantage of foraging in groups.

Many studies have found that individuals foraging in groups spend less time in vigilance (e.g. Elgar and Catterall 1981) and therefore, have more time for other behaviours such as feeding and observing others (see review by Elgar 1989). By observing where others are foraging, individuals can obtain an increased feeding efficiency by profiting from their food finds (e.g. Krebs et al. 1972, Custer and Osborn 1978, Giraldeau and Lefebvre 1986, Senar and Metcalfe 1988). This has been shown experimentally in birds (Benkman 1988) and in fish (Pitcher et al. 1982) where feeding in groups reduces the time required to find patchily-distributed food as individuals are attracted to the patches of successful foragers.

Advantages of Mixed Species Group Foraging

All the studies mentioned above have been on single species foraging groups, but the same advantages have been applied to mixed species foraging groups (e.g. Krebs 1973). In an experiment on starlings, Powell (1974) found a reduction in time individuals devoted to surveillance and a quicker response to a flying hawk model when they foraged in groups. The same results occurred whether the starlings foraged with a group of conspecifics or a group of blackbirds.

Both reduced predation risk and an increased feeding efficiency were proposed as advantages for mixed species foraging groups in Morse (1970).

1 and Short (1961) Cody (1971) theorized that feeding efficiency, defined as food intake per bird per unit time increased in mixed species flocks, because individuals avoided feeding in areas previously visited by others and therefore maintained a greater contrast of food abundance between foraging sites

Competition in Foraging Groups

Species which are normally found together in mixed flocks are those which are most similar in their foraging ecology (Morse 1970) This is illustrated by Pulliam and Enders (1971), who found complete dietary overlap in five finch species foraging together. Competition over food resources should exist whenever the use of a resource by one individual reduces the amount available to another, either of the same species (intraspecific competition) or of a different species (interspecific competition) (Wittenberger 1981)

Competition can manifest itself through either resource depletion or aggression with competitors. The former has been called scramble competition as it occurs when a bird competes through speed such that the faster it eats, the more food it obtains (Clark and Mangel 1986). The latter has been called interference competition as it occurs when one bird interferes with another's access to a necessary resource, usually due to territoriality (Miller 1967). Benkman (1988) suggested that when in large flocks, crossbills may increase their rate of seed consumption to reduce the effect of seed depletion by others in the flock. Scramble competition may also be the reason that phalaropes peck three times faster when feeding with shovellers than they do when feeding alone, and twice as fast as they do when feeding with conspecifics (Siegfried and Batt 1972).

Interference competition limits social interaction and thus limits the benefits associated with foraging in a group. While many territorial species exhibit interference competition towards conspecifics, this type of competition is harder to find in mixed species foraging groups, where aggression is more commonly used in the defense of reproductive areas than in foraging (Hinde 1956). Therefore, mixed species groups may form in cases where the advantages associated with group foraging cannot be achieved in homospecific foraging groups because of aggression.

Composition of Mixed Species Foraging Groups

Some mixed species flocks have been described as containing two main components, a nucleus species and an attendant species, following the original classification by Winterbottom (1943). The one or more nucleus species are always highly gregarious and considered the core of the flock whereas the one or more attendant species are territorial and rarely number more than a few individuals. These mixed groups are formed by territorial species joining any gregarious species in their vicinity as they are not able to form independent conspecific groups on their own (Winterbottom 1943). There are many examples in the literature of mixed species flocks which fit this description (e.g. Rand 1954, Vuilleumier 1967, Buskirk et al. 1972). The classification also seems to fit the aggregations studied in the present thesis, which are composed of territorial Zenaida doves, highly gregarious Carib grackles, and moderately gregarious cowbirds. Ground doves and bullfinches (French 1973, Devas 1970, Lefebvre MS).

It is conceivable that when Zenaida doves forage with heterospecifics, they obtain benefits of group foraging that cannot be obtained through homospecific foraging groups. Among these benefits, avoidance of predation seems less likely than foraging information. Individuals can only benefit from early predation warnings from members of a mixed species foraging group if the information is transmitted to them and if all members of the group are alert for the same predators (Metcalf 1984). During the field study however Zenaida doves were often observed to fail to respond to flight and alarm calling responses of the grackles they were foraging with. This occurred frequently in the presence of cats which were numerous in certain areas.

Two independent field studies mentioned earlier have produced anecdotal evidence that interspecific social learning of foraging behaviours can occur in mixed foraging groups of the type Zenaida doves belong to. In the first study a territorial species, the sunbird, was observed to forage with a gregarious species, the white-eye (Greig-Smith 1977). When white-eyes were present, sunbirds copied both where and how the white-eyes foraged. This resulted in increased feeding efficiency for the sunbirds and reduced intraspecific aggression. In a similar example a territorial species, the robin, was found to copy the foraging techniques and food choice of a gregarious species, the Cedar waxwing. When foraging together, robins imitated the waxwings by hovering to feed on juniper berries (Maclean 1970).

Predictions

In the present study, foraging associations and interactions are recorded between Zenaida doves and all other species with which they are found to forage. The aim of the field study is to determine the intra- and interspecific potential for social learning that exists in these mixed species aggregations. The foraging interactions which are important in this context are of two types: (1) aggression, which presumably interferes with social learning and separates animals from one another, (2) joining, which brings foraging animals closer together. Since Zenaida doves are territorial (Lefebvre MS), high levels of intraspecific aggression can be expected whenever conspecifics are encountered during a foraging bout. Conversely, if Zenaida doves join mixed species groups to obtain the feeding information benefits they do not obtain from conspecifics, we can expect low levels of interspecific aggression and a high frequency of interspecific joining. The net result of these two trends should be a high frequency of association of Zenaida doves with heterospecifics and a low frequency of association with conspecifics.

Methods

The study was based at the Bellairs Research Institute of McGill University, Barbados, West Indies. Field observations were collected from March to June 1989 at five sites on the west coast of the island (Figure 1). This period corresponded to the middle of the dry season. Three of the five sites consisted of hotel grounds (Coral Reef Club, Divi St. James and Heywoods), one was a public park (Folkstone) and one a residential area (Sunset Crest). Animal numbers, availability of roosting and nesting areas, amount of natural and human-provisioned food and risk of predation all appeared to vary between sites.

Two sets of data were recorded: a series of trials using provisioned food sources and a series of trials without provisioning. Provisioning, through the enhancement of the food supply, was expected to increase the frequency of interactions between Zenaida doves and the other species with which they forage. Trials without provisioning were designed to control for the effects of an increased food supply.

In each provisioning trial, nine patches of food were set out in a 3x3 array, with 2 m separating adjacent patches. Each patch consisted of 5 g of cooked white rice spread over a 50 cm² area. Preliminary experiments had shown that this food type was readily eaten by both Zenaida doves and the four species with which they can be found foraging. Trials started when a bird began feeding and lasted until the food supply was depleted or until all birds had ceased feeding. Data were only recorded for the birds foraging at the patches of food, which often fell within the boundaries of a single Zenaida dove territory. Therefore, to cover the territories of different individuals, trials were run at four different areas in each of the five sites for a sample size of 20 areas. Within a site, areas were separated by approximately 50 m.

Unprovisioned trials were conducted at the same five sites as the provisioned trials. During unprovisioned trials data were recorded on all birds within view from an observation point and were not restricted to the 16m² defined by the food patches in the provisioned trials. At each site, unprovisioned trials thus encompass a larger surface than each of the areas-within-sites of the provisioned trials, but do not necessarily cover all four areas that were provisioned on the site.

Observations of each provisioned area ($n=20$) consisted of five replicate trials while observations of sites not involving provisioning consisted of four replicates. Each set of replicates for a given area or site was conducted on consecutive days at a rate of one trial per day.

The 20 unprovisioned trials lasted 50 minutes each and involved recording the same data as in the 100 provisioned trials. The total time spent observing these interactions was designed to match the approximate total duration of the 100 provisioned trials, which lasted on average 9.34 minutes each. All trials were run between 05:30 and 08:00 EST. Data were collected from the provisioned trials first, followed by the unprovisioned trials.

Identical dependent variables were recorded in provisioned and unprovisioned trials by a team of two observers. Using a 30 second scan sampling procedure (Altmann 1974), one observer recorded all foraging associations. In the provisioned trial, this was done by recording the number of individuals of each species foraging together at each of the nine food patches. In the unprovisioned trials, all foraging birds were recorded along with the composition of all foraging groups, where a foraging group was defined as any birds foraging within one body length of another. The other observer noted on a continuous basis each occurrence of joining and aggression performed by or towards a Zenaida dove. Joining was defined as walking or flying towards a foraging bird and feeding within one body length. In the provisioned trials, joining was restricted to birds feeding at one of the nine piles of food. Aggression was defined as chasing, pecking, pulling or wing-slapping another bird; threat displays were excluded from this definition because low-intensity forms were often difficult to notice.

Observations were spoken into cassette recorders and later transcribed onto data sheets. In order to determine the accuracy of these observations, three provisioned trials were repeated halfway through the data collection and videotaped. Recording data verbally into tape recorders was found to be, on average, 94% as accurate as videotaping: for example, 51 joining and aggression events between doves and grackles were seen on the video record, 48 of which had been correctly recorded during the trials.

In order to compare the number of birds present in each trial, the average number of each species present per scan was calculated. This was done by summing the number of each species present in each scan and then calculating a mean scan for each trial. To compare foraging interactions, the

frequency of each was summed for each trial. Four types of foraging interactions were examined in the analysis: frequency of doves joining doves (intraspecific joining), frequency of doves joining heterospecifics (interspecific joining), frequency of aggression between doves (intraspecific aggression), and frequency of aggression between doves and heterospecifics (interspecific aggression).

Results

1 - Provisioned Trials

Overall Trends

Provisioning attracted large numbers of birds to the food sources. Table 1 provides the average number of birds per scan for each of the five species present. Carib grackles were by far the most numerous with a mean of 7.86 birds per scan. They also provided almost all of the heterospecific joining and aggression events that involved Zenaida doves. Over the 100 trials, there were 401 occurrences of a dove joining a feeding grackle and only 207 occurrences of a dove joining a feeding conspecific. Aggression showed a completely opposite pattern, as 1374 of the 1391 attacks and chases recorded occurred between Zenaida doves. The overall rates of joining and aggression were respectively 0.59 and 1.30 events per minute per dove. Since grackles are by far the most important heterospecific foraging associate of Zenaida doves (94% of interspecific joining and 100% of interspecific aggression), the rest of the analysis will focus on this species and exclude bullfinches, cowbirds and Ground doves.

Foraging Associations

The consequence of the opposing pattern shown by dove-dove and dove-grackle interactions is illustrated in Figure 2. One scan was randomly sampled from each of the 100 trials and the number of food patches in each scan with the following group compositions were counted: a dove foraging alone, a dove foraging with one or more conspecifics, a dove foraging with one or more grackles, and a dove foraging with one or more conspecifics and grackles. In the vast majority of cases, Zenaida doves were found to forage either alone (0.50 patches or 50% of occupied patches) or with grackles (0.38 patches or 38% of occupied patches). Zenaida doves were seldom found foraging with conspecifics, either with or without grackles.

Relationships Between Variables

In the following sections, the results will be analyzed using lumped data for the five replicate trials per area. The 20 areas will be treated separately, since they were designed to represent the territories of different resident Zenaida doves. By using variation over these 20 areas, the relationship

between aggression, joining and the number of birds present can be examined in more detail. Scatter diagrams of these relationships are provided in Figures 3-8. A Spearman rank correlation coefficient was calculated for each relationship and the result (r_s) and its significance level is provided in each graph. A non-parametric estimate of the relationship was preferred because of the nested (5x4) spatial structure which could affect the normality of the error distribution.

The frequency of aggression between doves was positively correlated to the frequency of doves joining doves ($p < 0.01$) (Figure 3). However, both of these variables were positively correlated to the number of doves present ($p < 0.01$) (Figure 4A & 4B). In order to see if this effect alone could explain the relationship between aggression and joining, both variables were divided by the number of doves present. Aggression per dove and joining per dove were still found to be significantly related ($p < 0.05$) (Figure 5).

Similar results were found in dove-grackle interactions. The frequency of aggression between doves and grackles was positively correlated to the frequency of doves joining grackles ($p < 0.05$). However, this relationship was not as strong ($r_s = 0.47$) (Figure 6) as the one found between doves ($r_s = 0.89$) (Figure 3). Neither aggression nor joining were related to the number of grackles present (Figure 7A & 7B). In Figure 7A, the apparent downward curvilinear trend in the data does not reach significance when tested against a quadratic polynomial regression. Not surprisingly, when the effect of the number of grackles was removed, interspecific aggression per grackle was still positively correlated to interspecific joining ($p < 0.01$) (Figure 8).

Absolute vs Relative Frequencies of Interactions

From the absolute frequencies presented in Table 1, it would be tempting to conclude that Zenaida doves preferentially join grackles and are preferentially aggressive to conspecifics. These frequencies do not take the number of birds present into account, however, and it is conceivable that doves are simply addressing behaviours according to the number of birds encountered, irrespective of species. To test for this, expected frequencies for joining and aggression were calculated and compared to observed frequencies using a Chi Square test.

Two different null hypotheses were used to calculate these expected frequencies of joining. Table 2 illustrates the results achieved by each method.

assuming that on arrival, a dove can join either of 3 patches occupied by the following hypothetical foraging groups: one dove, 15 grackles, and three grackles (Example 1)

The first method uses the total number of doves and grackles present. If there are three patches of food with a total of 1 dove and 18 grackles, then there is a 5% chance of a dove joining a conspecific and a 95% chance of a dove joining a grackle. Therefore, 5% of all observed joining events would be expected to be towards a dove (intraspecific) with the other 95% expected to be towards a grackle (interspecific).

The second method uses the species present at each patch, assuming that doves are not attracted to a patch purely on the basis of the number of birds that are there. In this example, a dove going to patch A can only encounter conspecifics, while a dove going to patches B or C can only encounter heterospecifics. There is therefore a probability of 0.33 of joining or directing aggression to a dove when arriving at one of the three patches, and a probability of 0.66 of joining or directing aggression to a grackle. If a patch contains more than one species, only the results of the second method are affected (Example 2). In this case the unit allotted to the patch is divided according to the number of birds of each species present. If patch A has one dove and one grackle, there is an equal probability of 0.5 of joining or directing aggression to a dove or a grackle at that patch. If patches B and C contain only grackles, then the probability of a dove joining or directing aggression to a conspecific at one of the three patches is now 0.17, and the probability of joining or directing aggression to a grackle is 0.83. This is the case described in the lower part of Table 2.

1- Joining Behaviour

For joining, the results using expected frequencies based on the total number of birds present (Method 1) are shown in Figure 9. A heterogeneity Chi Square test (Zar 1984) determined that the areas differed significantly ($X^2 = 128.64$, $p < 0.001$), thus reinforcing the earlier a priori decision to treat the 20 areas separately. In nine areas, doves joined conspecifics significantly more than would be expected based on the number of doves present, and therefore joined grackles significantly less than would be expected based on the number of grackles present. In the other 11 areas, joining was not significantly addressed to either species.

The results using expected frequencies based on the type of species present at each food patch (Method 2) are shown in Figure 10. A heterogeneity Chi Square test determined that the areas again differed significantly ($X^2 = 31.28$, $p < 0.001$). In the majority of areas (17/20), doves joined randomly, regardless of species. In the other three areas, doves joined conspecifics significantly more than expected, and hence joined grackles significantly less.

2- Aggressive Behaviour

Since acts of aggression were not restricted to birds feeding at the food patches, but could occur anywhere in the vicinity of the food, expected frequencies of aggression were only generated according to the total number of doves and grackles present in each of the 20 areas (Method 1). A heterogeneity Chi Square test again determined that the 20 areas differed significantly ($X^2 = 2271$, $p < 0.001$).

In 19 of the 20 areas, aggression occurred between doves significantly more often and therefore between doves and grackles significantly less often, than expected ($p < 0.001$) (Figure 11). In the last area (Area #13), there was no aggression recorded.

2 - Unprovisioned Trials

Overall Trends

The data obtained from the 5 sites where unprovisioned foraging associations were recorded confirm some of the previous descriptive patterns, but also reveal some important differences (Table 3). The average number of birds per scan (7.02) and the overall rates of both joining (0.06 events/dove/minute) and aggression (0.13 events/dove/minute) were lower, as can be expected from the lower amounts of food available due to lack of provisioning. Grackle numbers in particular were low, which is reflected in a lower absolute frequency of doves joining grackles (81) as compared to the frequency of doves joining conspecifics (123). As in the provisioned trials, aggression occurred almost exclusively between Zenaida doves (468 of 478 cases). Bullfinches, cowbirds and Ground doves combined again represent a small percentage of the interspecific joining and aggression observed (16% and 0% respectively). Further analyses will thus focus only on the interactions between Zenaida doves and grackles, and will use the same nonparametric tests as above, due to the possible non-normality of the data.

Foraging Associations

As with the provisioned data, 100 scans (20 per site) were randomly chosen from the data and the number of foraging groups containing the following were counted: a single dove, a dove with conspecifics, a dove with grackles or a dove with conspecifics and grackles. The consequence of low grackle numbers and high rates of dove-dove aggression is that Zenaida doves were almost always found foraging alone: 89% of the foraging groups contained a single dove (Figure 12).

Relationships Between Variables

When the relationships between joining, aggression and the number of birds present are examined over the five sites, we find partial confirmation of the trends that appeared in the provisioned trials. For instance, intraspecific aggression is significantly correlated with the number of doves present (Figure 14B), the trends fail to reach statistical significance in several cases, however, which is not surprising given the low sample size ($n=5$) (Figures 13, 14A, 15, 16, 17B & 18). Contrary to provisioned trials, there was a significant

positive correlation between the number of grackles present and the frequency of interspecific joining (Figure 17A).

Absolute vs Relative Frequencies of Interactions

The observed frequencies of joining and aggression were compared to the frequencies generated on the basis of the number of birds present. In this case, no alternative null hypothesis is available, since joining is not restricted to defined patches of food.

1- Joining Behaviour

There was no significant difference between the observed frequencies of doves joining conspecifics or grackles and those expected by chance (Figure 19). Therefore, in the unprovisioned samples, doves were joining randomly, regardless of species, in every site.

2- Aggressive Behaviour

In three of the five sites, aggression occurs between doves significantly more than would be expected based on the numbers of doves present (Figure 20), as was found in the provisioned trials.

Discussion

The main results of the field study can be summarized in three points. (1) in terms of absolute frequencies, doves join grackles more often than they do other doves when provisioning attracts large numbers of grackles, when there is no provisioning and grackle numbers are low, doves join conspecifics more often, (2) in terms of both absolute and relative frequencies, doves preferentially direct aggression to conspecifics, whether provisioning occurs or not; (3) in terms of relative frequencies, doves join conspecifics and grackles in proportion to the number of birds present in all unprovisioned sites and in most of the provisioned areas, in the rest of the provisioned areas, doves preferentially join other doves

Provisioning had both expected and unexpected results. As predicted, the artificial increase in amount of food available led to a ten-fold increase in the rate of joining and aggression seen per dove (respectively 0.06 and 0.13 events/minute/dove to 0.59 and 1.30). Provisioning also seemed to attract grackles in larger numbers, as evidenced by the observed tripling of the number of grackles per scan. Provisioning additionally had the apparent effect of lowering Zenaida dove numbers, but this effect is probably a spurious consequence of the spatial definition of the scanning area in the two types of trials. In unprovisioned trials, the area corresponding to a scan is much larger than the one used in provisioned trials and usually includes more than one Zenaida dove territory. Since grackles are not territorial and move in groups to whatever food resource is available with a site, their numbers are much less biased by the spatial definition of the scan.

The unexpected result produced by provisioning lies in the reversal of absolute joining frequencies that accompanies the change in grackle numbers. When grackles are numerous, as they are during provisioning, doves join them twice as often as they do conspecifics. When grackles are rare, as in unprovisioned trials, doves join conspecifics 1.5 times more often than they do grackles. This shift is consistent with the relative frequencies shown at the majority of sites when animal numbers are taken into account: doves seem to randomly join whatever species is present. Thus, although the amount of food available in provisioned trials is somewhat higher than normal, the behavioural changes that follow this increase in resources fit a logical pattern and strengthen the conclusions of the analysis on relative frequencies.

In provisioned trials, it should be recalled that two different methods were used to generate the expected values of the relative frequencies. One method was based on the number of birds present per species, the other one on the number of patches occupied by each species. The methods lead to the same conclusion in 14 out of 20 areas. In six cases, however, results that suggest selective joining of conspecifics according to Method 1 suggest random joining according to Method 2. Since the first method probably overestimates the attractive effect of grackles and the second method probably underestimates it, a cautious interpretation of the results should focus on the average picture provided by the two techniques. Method 1 assumes that the tendency to join is a monotonic function of the number of birds present at a patch. 25 grackles will provoke more joining than three grackles, who in turn will attract more joining than a single grackle. This assumption is reasonable at low numbers, but may not hold when birds become so numerous that access to the patch and the food it contains becomes difficult. Tendency to join may instead be a curvilinear function (inverted-U) of the number of birds present, as in the Allee type models of animal distributions (Fretwell 1972). The difficulty in determining the inflexion point of this curve, however, makes this model theoretically interesting but empirically useless. In the absence of extended observations to determine beyond which numbers doves are repelled rather than attracted to a patch attended by grackles, the methods used in this thesis can provide reasonable estimates of the null hypothesis.

The second method used here, the calculation of expected frequencies based on the number of patches occupied by a given species, is not subject to the problem described above. The method assumes that the probability of joining a species depends on the number of patches occupied by that species, whether one, five or 15 birds are at a given patch. It is thus insensitive to actual numbers per patch. If numbers do have an effect up to a certain unspecified value, the second method will underestimate the expected tendency for doves to join grackles. The correlation data on the relationship between joining and number of birds present are not very useful to decide which assumption is more realistic: joining of grackles is positively correlated with grackle numbers in unprovisioned trials (Figure 17A) but not in provisioned ones (Figure 7A), while joining of doves is significantly related to dove numbers in provisioned trials (Figure 4A), but not in unprovisioned ones (Figure 14A).

1 If we thus consider that the best estimate of expected frequencies lies somewhere between the ones yielded by the two methods, we can safely conclude that doves tend to join other birds on a random basis in a majority of cases. This majority lies somewhere between the weak one given by Method 1 (55% of areas) and the stronger one given by Method 2 (85% of areas). This conclusion is reinforced by the fact that data from unprovisioned trials show random joining in all areas and is further supported by the reverse in absolute joining frequencies discussed above.

Given these considerations, random joining associated with high intraspecific aggression seems to be the pattern that emerges from the field data. Grackles and doves thus appear to be equally attractive as potential sources of foraging information for a Zenaida dove, but the high level of intraspecific aggression may disrupt any effective transfer of this information. The consequence of aggression can be seen in the association data obtained from the two sets of 100 randomly chosen scans both in provisioned and unprovisioned trials. Zenaida doves rarely forage with a conspecific. When doves forage in the company of other birds, these birds are almost always grackles. Although the field study does not provide unequivocal support for the idea that social learning in Zenaida doves is mainly heterospecific, the combination of the association data, the aggression data and the joining data suggest that the conditions for interspecific learning are probably better than those for intraspecific learning.

3. PART B - LABORATORY STUDY

Introduction

Once it has been established that the potential for social learning exists in the field, it is necessary to study social learning under controlled laboratory conditions in order to determine what information can be transferred and between which birds. In Part A of this thesis, it was determined that doves joined other foraging doves or grackles as a function of the number of birds present, but were selectively aggressive towards conspecifics. When few grackles were present, this resulted in doves foraging most often alone, and when grackles were numerous, in doves foraging equally often with and without grackles. Therefore, based on frequency of association at a feeding site, grackles seem to represent the most stable source of foraging information for doves.

Data on joining behaviour alone cannot lead to a clear-cut prediction for the direction of social learning in a controlled experiment. This is because joining may inhibit transmission. Giraldeau and colleagues (Giraldeau and Lefebvre 1987, Giraldeau et al. 1990, Giraldeau and Templeton MS) have shown that an observer who obtains food during a demonstration (the cage equivalent of joining) often does not learn the searching technique of its demonstrator. In closed aviary groups, this may result in only a portion of the flock showing the required food searching technique, the rest of the birds learning instead which knowledgeable individuals to follow and join (Giraldeau and Lefebvre 1987). Beauchamp and Kacelnik (1991) have confirmed the presence of inhibitory effects of joining on individual learning of environmental contingencies. In field conditions, this learned producer-scrouter relationship (Barnard and Sibly 1981, Giraldeau 1984, Giraldeau and Lefebvre 1986) may or may not lead to inhibition of social learning, depending on the rate of emigration of knowledgeable birds and the rate of immigration of naive ones (Lefebvre 1986, Lefebvre and Palameta 1988). Whether or not these factors affect the relationship between joining and social learning in dove-grackle encounters is unknown.

In the present case, it is thus important to consider the net effect of joining and aggression when designing experiments on the basis of the field data. Because of the random pattern shown in the field data and the potential inhibitory effect found by Giraldeau, joining is of little use in establishing

predictions for the experiments. The data on aggression however, suggest that any potential transfer of information between doves is likely to be disrupted by aggression and that the net intraspecific effect of high aggression and moderate joining is that doves rarely end up foraging next to other doves. However, doves do commonly forage near grackles when they are present. Therefore, grackles represent the main stable source of foraging information available to the doves. It is therefore more likely that grackles will be used as sources of information in controlled experimental conditions.

Description of Laboratory Study

In part two of the thesis, two experiments were designed to test doves for demonstrator preference in social learning. Both tasks were similar to naturally occurring foraging problems. Experiment One tested demonstrator preference (grackle versus conspecific) in a choice test of novel foods. In this experiment, the naive doves could indicate whether they preferred to copy a conspecific or a heterospecific in deciding which of two novel foods to eat. Novel foods were created by colouring cooked rice, the same food that was used in the field trials. Preliminary experiments and training of dove demonstrators had shown that naive doves will not readily approach these foods without other birds showing them that the foods are edible.

Experiment Two was designed to test the doves' capacity to learn a novel food-finding problem from either a heterospecific or a conspecific demonstrator. In this experiment, the naive doves could apply a known motor act, pushing, to a novel stimulus, a lid covering food inside a box. Using the beak to push aside obstacles such as leaves or sand obstructing access to food is a commonly observed technique in *Zenaida* doves (pers. obs.).

In both experiments the tasks are sufficiently similar to normally occurring behaviours to be ecologically relevant, while being sufficiently artificial for them not to be already known by the animal. Although no control groups were used to compare the rates of social learning and individual learning, demonstrators were initially trained individually using shaping. Grackles accepted the novel foods within minutes after they were presented. However, the doves were reluctant to eat the novel foods, and it took more than a week of daily presentations before they would eat. When other dove demonstrators were allowed to observe the grackles feeding during their presentation of the novel foods, their latency to eating was reduced to a couple

of days. The same was found to occur when training the demonstrators to push a lid off a hole in a box to obtain the food inside.

Experiment 1

Methods

For the experimental study, doves and grackles were wild-caught in walk-in traps which measured 30 cm x 30 cm x 30 cm. The cages were built out of wood frames (2.5 cm²) and 4 cm round chicken wire for the doves and 1 cm square chicken wire for the grackles.

For Zenaida doves, the trapping procedure involved placing a caged dove in a resident bird's territory, adjacent to an empty cage with the door open. Once the resident dove was attracted, all sides of the two cages were covered with pieces of pressboard (30 cm²) except the entrance. This provided the dove with only one way of reaching the intruder, i.e. through the empty cage. This was found to be the most effective means of trapping doves, as resident doves were quickly attracted to the intruding dove and enticed into the empty cage with food. The closing of the trap was controlled manually by a string attached to the door of the cage. Grackles were attracted into the traps by placing food inside. The birds were trapped in a variety of locations from each of the different sites in which the field data were collected.

Once caught, the birds were tagged with coloured and numbered leg bands, weighed, and housed individually in the same cages used as traps. A bowl of water was placed inside each cage, providing the birds with access to a supply of clean water at all times. The cages had one wall with 3 large openings (enlarged chicken wire) through which the birds could reach petri dishes (50 cm²) with food placed outside the cage. The birds were fed an ad libitum diet of mixed finch seed, bread crumbs, and rice. The diet of the doves was occasionally supplemented with cooked egg for extra protein. The grackles required a greater quantity of protein in their daily diet, so in addition to the above, they were fed cooked chicken and beef and the occasional wild-caught lizard.

The experiments were run in an outdoor aviary located on the grounds of the Bellairs Research Institute of McGill University, in Barbados, West Indies. The aviary was originally a roofed concrete tank (2.4 m x 4.5 m x 3 m) which was modified into an enclosed area by constructing walls out of wood and 4 cm round chicken wire. The walls were covered with layered palm fronds to keep the interior of the aviary shaded and isolated from disturbances.

A table (0.8 m x 1.2 m) was set up at each end of the aviary on which the experiments were run. The two experimental areas were separated by a curtain, which functioned as a blind during experiments and as a visual barrier between the birds on each table (Figure 21).

The objective of the first experiment was to determine the naive doves' preference for either the food type eaten by a conspecific or the one eaten by a grackle. Two doves and two grackles were trained as demonstrators of the novel food, which was cooked rice coloured either red or green with commercial food dye. The novel foods, mixed with plain rice, were presented to both the dove demonstrators and the grackle demonstrators. The grackles ate the rice quickly, but the doves pecked at it only after being able to observe the grackles.

Once all four demonstrators were familiar with the foods, they were placed on the experimental tables in the following set-up: one grackle demonstrator and one dove demonstrator were placed side by side on each table, facing a naive dove observer. The observer's cage was positioned directly opposite the midline separating the two demonstrators' cages (see Figure 21). The naive dove therefore had constant visual contact with both demonstrators during the presentation part of the trials. There was no overt aggression between caged doves, nor was there a tendency to avoid the side of the cage closest to the dove demonstrator.

During the experiments, the doves' weights were reduced on average to 85% of their maximum weight, measured either upon capture (free ranging weight), or after *ad libitum* feeding. Before a trial, each naive dove was placed in an experimental set-up and food deprived for approximately 20 hours. This ensured that the birds were sufficiently motivated and habituated to the demonstrators before each session. All sessions were conducted between 10 am and 4 pm. The birds were only fed during the experiments or shortly afterwards, and then with just enough food to maintain their stable weight, which was assessed on a daily basis.

Each naive dove was given a five minute demonstration of the dove and grackle demonstrators simultaneously eating one of the two colours of rice presented in a petri dish (Figure 22). All naive doves had experience eating out of petri dishes, for an average of two days prior to being tested. Of the 30 naive doves tested, 15 observed the grackle demonstrator eating red rice and the dove demonstrator eating green rice, while the other 15 observed the

reverse. After the five minute demonstration, the demonstrators' food was removed and a barrier was placed between the naïve dove's cage and the demonstrators' cages. The naïve dove was then presented simultaneously with the two colours of rice, each one offered on the same side of the cage as its demonstrator's was (Figure 22). The observer had five minutes to choose one of the colours. A preference was determined by the coloured rice which was first pecked at. If no choice was made after five minutes, the food was removed and the trial repeated. Once a colour was pecked at, the food was immediately removed and the trial was repeated once to test for stability in choice. A maximum of 10 trials per day were given for up to five consecutive days, or until two consecutive food choices were made. Two birds were tested per day.

Experiment 1

Results

The results of Experiment 1 are given in Figure 23. Of 30 doves tested, 21 chose the colour of rice eaten by the grackle demonstrator, while 9 doves chose the colour eaten by the dove demonstrator. This is significantly different from random when tested with a Chi Square test with Yates' correction for continuity (Zar 1984, $X^2 = 4.034$, $p < 0.05$).

However, this analysis only takes into account the first choice made by the doves and cannot rule out the possibility that observers are simply trying both food types in succession. Each observer was thus given one additional trial after first pecking at the rice to determine how stable its choice was. The results taking into account both choices are illustrated in Figure 24. Of the 30 doves tested, two made unstable choices. One of these doves copied a dove demonstrator on its first choice and then copied a grackle demonstrator on its second choice while the other dove did the opposite. Overall, 20 doves copied a grackle on both choices, 8 copied a dove on both choices, and two made unstable choices.

Expected frequencies for each of the three categories were determined from combined random probabilities. If choice is random, there is a 0.5 chance of copying either demonstrator on Trial 1, and a 0.5 chance of doing so on trial 2. Therefore, there is $0.5 \times 0.5 = 0.25$ chance of copying the same demonstrator species on both trials. There is a $0.25 + 0.25 = 0.5$ chance of making an unstable choice, from a 0.25 chance of choosing a dove and then a grackle, plus a 0.25 chance of choosing a grackle and then a dove. Using these probabilities to calculate expected frequencies, a significant difference was found with the observed frequencies in a Chi square analysis ($X^2 = 32.13$, $p < 0.001$). Therefore, doves chose to eat a novel food demonstrated by a grackle significantly more often than a novel food demonstrated by a conspecific.

This result occurred regardless of differences in pecking rate. For example, in 10 randomly chosen observer/demonstrator pairings, 7 doves observed a dove demonstrator eating more than a grackle demonstrator, but 6 of them copied the grackle. In the remaining three cases the grackle demonstrator was observed to eat more than the dove demonstrator, while the naïve doves chose the food eaten by the grackle.

As shown by Figure 25, neither colour of rice was preferred by the observers ($X^2 = 0.84$, N.S), and as illustrated by Figure 26, there was no interaction between the colour of rice chosen and the demonstrator of that colour, as determined by a 2 x 2 contingency table ($X^2 = 0.63$, N.S)

Experiment 2

Methods

In the second experiment, the doves were required to learn a novel task, pushing a lid off an opening in a box to reveal food inside. The lid was a black plastic jar cover, 5.5 cm in diameter and 1 cm high. The box was constructed out of pressboard and measured 7 cm x 7 cm x 3.5 cm with a hole (1 cm deep) cut in the top, 5 cm in diameter.

The same subjects and demonstrators were used as in the first experiment and no changes were made to the aviary or experimental set-up (Figure 27). Demonstrators were trained to push the lid off the box by starting with the lid partly covering the food and then progressively covering the entire hole. The naive doves were allowed to habituate to the food box for an average of two days before the experiment by having their food presented in the box without the lid. This procedure was similar to the first experiment where the doves were presented their food in petri dishes before and during the experiment.

During the demonstration phase of the second experiment, one bird pushed a lid off and fed from a box while the other one fed from a petri dish. Both contained the same food, mixed seed and cooked white rice. Of the 22 doves tested, 11 observed a grackle demonstrator pushing a lid and a dove eating from a petri dish and 11 observed the opposite. In each five minute demonstration, the demonstrator with the box could only flip the lid once and eat from the box, while the other demonstrator simultaneously ate from the petri dish.

The demonstrators' food was then removed and a barrier placed between the observer and the demonstrators. The naive dove was then offered a choice between a box with a lid and an empty petri dish, arranged to coincide with the side of their demonstrators (Figure 27). As in the first experiment, observers were given a maximum of 10 trials a day for five consecutive days. Testing was terminated if an observer succeeded in removing the lid and eating on two consecutive trials. After 50 unsuccessful trials, the observer was considered unable to perform the task. In addition to lid removals, pecks at the empty control dish were recorded for each dove. After the termination of Experiment two, all birds were fed ad libitum and set free.

Experiment 2

Results

The results from Experiment 2 are summarized in Figure 28. The left side of the graph (A) represents the number of doves that did or did not learn from their demonstrator to remove the lid and eat from the box. Of the 11 doves that observed a grackle demonstrator push the lid and eat, 7 learned, while only 1 dove out of 11 learned after observing a dove demonstrate the task. Ten doves observing a dove demonstrator push the lid did not learn, as compared to only 4 doves not learning from the grackle demonstrator. When tested with a 2x2 contingency table (Zar 1984), there was a significant relationship between the number of doves that learned to eat from the box and the demonstrator they learned from ($\chi^2 = 4.92$, $p < 0.05$, $n=22$).

More surprisingly, grackle demonstrators seemed to influence observers even when they provided the inappropriate information. The right side of Figure 28 (B) represents the number of doves that pecked at an empty petri dish rather than at the lid covering the food. When a dove demonstrator was removing the lid and a grackle demonstrator was eating from a petri dish, five doves pecked at the empty petri dish. When the demonstrators were reversed and a dove demonstrator was eating from a petri dish, no doves pecked at their empty petri dish. There is a significant relationship between the number of birds which pecked at the empty petri dish and the demonstrator they observed eating from a similar open dish ($\chi^2 = 10.05$, $p < 0.01$).

Discussion

Experiment One - Food Choice

In the first experiment, each demonstrator provided the same type of information, the edibility of a novel food. Both the grackle and dove demonstrators ate out of petri dishes, both were given the same amount of food and the same type of food, with the only difference being the colour of the food. From the results of this experiment, it is clear that doves preferentially copied the grackles' food choice (Figure 23), even on two consecutive choice tests (Figure 24). This finding is further strengthened by preliminary tests which found that doves appeared to prefer red rice over green and blue rice when given a choice without any previous demonstration. However, when a demonstration was shown before a colour choice test, there was no colour preference found overall (Figure 25) and there was no relationship between the number of doves copying each demonstrator and the colour demonstrated (Figure 26).

Experiment Two - Food-Finding Task

In the second experiment, each demonstrator provided different types of information. The same type of food was eaten, but this was presented in two different food dishes, a lid-covered box or an open petri dish. Previous to the experiment, all naïve doves had experience eating this food out of both uncovered boxes and petri dishes. Therefore, the only new information to be learned was how to reach the food inside the box, i.e. how to remove the lid. One demonstrator provided the necessary information for the observer to obtain food, while the other demonstrator provided irrelevant information, since each observer was then given a choice between a lid-covered box and an empty petri dish.

The doves appeared to be more capable of using the food-finding information when it was provided by a grackle (Figure 28A). Even more surprisingly, almost half the doves that observed a dove demonstrating the lid-pushing task (and therefore observed a grackle eat from a petri dish), pecked their empty petri dish rather than the lid covering the food. No doves pecked the empty petri dish after observing a dove eat from a petri dish (Figure 28B).

Overall, the naïve doves were found to direct their foraging behaviour towards stimuli that most closely resembled the stimuli their grackle

demonstrator interacted with. When shown the correct stimulus (the lid-covered box) by a dove demonstrator, and the wrong stimulus (the petri dish) by a grackle demonstrator, the naïve doves preferentially chose to interact with the stimulus associated with the grackle, regardless of its usefulness to obtain food

Previous Work on Zenaida Doves

The present results can shed some light on those previously obtained on Zenaida doves by Lefebvre and Palameta (MS). They confirm the earlier finding that Zenaida doves are capable of social learning, but suggest that the identity of the demonstrator species rather than stress associated with experimentation may explain the poor performance of doves in one of Lefebvre and Palameta (MS)'s experiments. In their experiment 1, Lefebvre and Palameta (MS) brought wild-caught Zenaida doves to the laboratory and gave them lid removal demonstrations by a conspecific.

Only 4 out of 15 observer doves later solved the lid removal problem. However, Zenaida doves were also poor in learning the lid removal problem by shaping in the absence of a demonstrator. In Lefebvre and Palameta (MS)'s experiment 2, Zenaida doves were pre-trained on a simple variant of another food-finding problem, removing the stopper on a tube containing seed. Doves were then either informed or not by a conspecific demonstrator that a change in technique was now required to remove the stopper. Only under these conditions of extensive pre-training could Zenaida doves be shown to imitate, in the sense that the group that was informed of the change modified its behaviour much more quickly than the uninformed birds who could only rely on feedback from the apparatus. Following these results, Lefebvre and Palameta (MS) conclude that extensive pre-training of the type given in experiment 2 (but not in experiment 1) is required to reduce the stress of captivity and testing, and allow Zenaida doves to show their potential for imitation.

However, the present results suggest that low number of doves learning in Lefebvre and Palameta (MS)'s first experiment could be due to the fact that conspecifics were used as demonstrators. The food-finding task in the present study is similar to the task of Lefebvre and Palameta's first experiment in the sense that both involved pushing a lid to uncover food. The proportion of observer doves learning from a conspecific is also comparably low in the two

studies 1 out of 11 here, 4 out of 15 in Lefebvre and Palameta's experiment. In both of these experiments, more doves succeeded in obtaining food through individual learning or from observing a heterospecific demonstrator than by observing a conspecific. Therefore, the conclusion of Lefebvre and Palameta that Zenaida doves require more habituation to testing conditions than do feral pigeons may be questioned. Lefebvre and Palameta (MS) may simply have used the wrong kind of demonstrator.

Mechanisms Involved

The precise mechanism responsible for the social learning obtained in this study is difficult to pinpoint, since the experiments were not specifically designed to discriminate between the various possibilities. As Palameta (1989) has shown, the best way to rule out simple mechanisms and demonstrate the existence of true imitation is to produce minute variations in the motor act required for solving a task and to control for all apparatus-linked cues associated with these variations. This was done in Lefebvre and Palameta's (MS) second experiment, and successfully showed that Zenaida doves were capable of imitating conspecifics.

In the present experiment, testing of observers was delayed until the demonstrators were out of their view. This procedure can rule out social facilitation, which requires simultaneous performance of the demonstrator. There is a specific form of local enhancement that the design used in this study cannot rule out, one based on a position effect. During observer testing, rice colours in experiment 1 and dish types in experiment 2 were placed in the same left/right position as they had been during the demonstration. As in practically all cage studies, observers were prevented from moving towards the place from which their demonstrator fed and therefore had to affect some kind of spatial transposition of what they saw to their own testing apparatus. A simple rule like "peck for food on the same side as the heterospecific demonstrator did" could suffice here, without any need to assume imitation or stimulus enhancement of the demonstrator's actual behaviour. This could also explain the apparently incorrect behaviour shown by the five doves who pecked at their empty food dish after seeing a grackle demonstrator eat from its open dish. In this case, the behaviour, in its initial stages at least, is clearly not maintained by food reinforcement nor guided by food-associated stimuli, since there is no food.

Natural shaping can also be ruled out. All observers had been given prior exposure to the open dishes they would later be tested with, but their response to testing reflected a clear demonstrator effect. Had natural shaping been sufficient, exposure to the dishes would have masked the variation seen in response to demonstrator species. Shaping may explain a portion of the learning effect but an additional social component is clearly required to account for the results.

This component could be local enhancement or true imitation. We know from the experiments of Lefebvre and Palameta (MS) that Zenaida doves, like pigeons (Palameta 1989) are capable of true imitation, so it is at least conceivable even in the absence of the required experimental controls, that imitation was used in the present case. Local enhancement cannot be ruled out empirically here and in cases where both it and imitation are not separated by precise technical procedures, animals may use both types of information: what parts of the environment to interact with and what motor acts to copy.

4. GENERAL DISCUSSION

Was the Hypothesis Supported?

The hypothesis tested in this study, that social learning in a territorial dove functions primarily in mixed species foraging groups, receives partial confirmation from the results of the field study and clear confirmation from those of the cage experiments. In learning both to feed on a novel food and to solve a novel food-finding problem, Zenaida doves clearly copied their grackle demonstrators even to the point of imitating the grackles' irrelevant behaviour while a conspecific demonstrated the relevant technique. This preference for grackles as informers of foraging behaviours is consistent with the high absolute frequencies of interspecific joining found in the provisioned field trials, coupled with the low levels of interspecific aggression and the high levels of intraspecific aggression. It is inconsistent with the shift to higher absolute frequencies of intraspecific joining when grackles become less numerous in the unprovisioned trials. This shift suggests that joining depends instead on the number of birds present, an interpretation confirmed by the analysis of joining rates relative to the proportion of each species present and the correlations calculated over the various field trials.

Two lines of argument suggest that the inconsistency may be more apparent than real. In the first place, indiscriminate joining by Zenaida doves often leads to short-lived, unstable aggregations when several doves end up feeding together. Intraspecific aggression will cause the aggregation to break up, as evidenced by the very low frequency of multiple dove foraging groups found in the average scan (Figures 2 and 12). Not only does intraspecific joining lead to unstable aggregations, it also creates poor conditions for information transfer. When aggression interrupts the foraging bout that follows joining, any information that is potentially transmitted is subject to being disrupted or incomplete. Even if adequate information is obtained, this may often prove useless, since intruding doves are chased by territorial residents and cannot feed on the food type and location they were attracted to. In a field situation, such instances of stimulus or local enhancement are likely to be the most frequently encountered sources of foraging information. Imitation of a new searching and/or handling technique is probably a much rarer occurrence than enhancement, though due to its possible cognitive implications, imitation has attracted considerable attention in the literature (see reviews by Galef 1976,

1988, Hauser 1988, Palameta 1989, Whiten 1989, Visalberghi and Frigaszy 1990a)

The second reason why random joining in the field is not inconsistent with selective copying of heterospecifics in captivity is that the information transmitted in the two cases is very different. The cage experiments were specifically designed to produce simultaneous and conflicting information coming from two different sources. In contrast, during the provisioned field trials, the information coming from different foragers was the same, since nine identical patches of rice were presented. Given that rice was not a novel food and that foraging trials were repeated in each location five times, the doves were not gaining new information each time they joined a patch. The foraging trials were not designed to test for social learning, but rather the potential for information transfer by determining foraging associations. In contrast, the cage experiments were designed to test for both the presence and direction of social learning.

In the unprovisioned trials, information was likely to be less homogeneous as the food sources available were not controlled. However, it is conceivable that information about food sources is most valuable to the doves when it is a novel and temporary rich food source in a clumped distribution. Often when these food sources are available, grackles are quickly attracted to the location. These situations then closely imitate what occurs during a provisioned foraging trial where there are many grackles and few doves present, and doves join feeding grackles more than conspecifics.

Indirect evidence from the present study suggests that one of the alternative hypotheses given in the introduction, the possible role of imitation in kin group foraging, is unlikely to explain the presence of social learning in Zenaida doves. In the random scan data taken both during provisioned and unprovisioned trials, doves were rarely seen to forage with other doves. These findings are consistent with those of Lefebvre (MS) and suggest that there is little potential for social learning to occur between mates or between parents and offspring, since these individuals seldom forage together. Although any definite conclusions on this hypothesis must await direct experimental testing, the evidence here points to the fact that kin group foraging is almost certainly less important than mixed species group foraging in providing a setting for the transfer of information.

Past Studies on Interspecific Learning

In the past, studies on interspecific social learning have fit into one of two categories. Some of the studies were simple anecdotal reports of one individual apparently learning to eat or avoid a novel food (Greenberg 1976, Rothschild and Ford 1968, Swynnerton 1942) or learning to obtain food using a tool (Millikan and Bowman 1967) by observing a heterospecific performing a similar behaviour. The rest of the studies compared the number of observers or the efficiency with which observers could learn a new foraging task depending on the demonstrator of that task (Turner 1964, Mainardi et al. 1972, Benel 1975, Sasvári 1979, 1985).

The results of these studies varied. Studying albino rats which observed a demonstration by either a Mongolian gerbil or a conspecific, Benel (1975) found no significant difference between the number of trials required for each group to reach their criterion. Sasvári (1979, 1985) found that more adult birds of various tit and thrush species could learn from conspecifics, but found no difference when juveniles were tested. Turner (1964) found that sparrows responded more weakly to chaffinches than they did to their own species when both performed the same foraging behaviours. Studying small mammals, Mainardi et al. (1972), found that more hamsters learned when shown a demonstration by a mouse (39%) than a conspecific (16%). It should be noted here that proportion of animals learning even in the most efficient condition is unusually low, suggesting that either the species or the task used by Mainardi et al. (1972) may be inappropriate.

In addition to the fact that the results of these studies are contradictory, the experiments themselves suffer from the problems mentioned earlier in the introduction. The present thesis is the only study of interspecific social learning where pairing of demonstrator and observer species is based on parallel field data. Choice of the heterospecific demonstrator used here was determined by association, joining and aggression frequencies in both provisioned and unprovisioned field observations. Grackles were chosen because they were clearly involved in more foraging interactions than the other three species encountered by Zenaida doves. An effort was also made in this thesis to devise ecologically-relevant foraging behaviours for the learning experiments. Finally, the counterbalanced design involving conflicting sources of information provided by the two demonstrators allows a more precise test of the hypothesis than the designs used in previous studies. For one, providing conflicting

information drastically reduces the probability that no difference will be found between heterospecific and conspecific demonstrators, since observers are forced to choose between the two solutions offered. Previous studies do not use this technique and it is thus possible that some reported failures to reject the null hypothesis are spurious because of this. Taken together, these arguments suggest that more adequate controls are needed to evaluate the significance of results obtained in other species and that the present study provides the clearest assessment of the ecological basis of interspecific social learning.

A Priori Expectations

The results obtained in this study may seem counter-intuitive. There is no reason to expect a priori that an individual should learn more easily from a heterospecific than from a conspecific. Even though past studies on interspecific learning have found variable results, logically, conspecifics should be more informative demonstrators because they have similar motor capacities and diets. Other species will never perfectly overlap in diet and may be capable of motor acts that are irrelevant or impossible for the naive individual to perform. In the case of Zenaida doves and grackles, these differences are even more pronounced as the latter is an omnivore with a diet ranging from plant matter to animal matter, including insects and lizards, as well as human food scraps (French 1973, Stamps 1983). Grackles also have a greater motor ability, being able to move their head and neck more than doves, and to use their beak for finer movements. Zenaida doves' beak movements are much more gross, most often involving pecking downwards or sideways. These differences were most obvious in preliminary experiments when a dove and grackle were allowed to interact with a box containing food covered with tissue paper held in place by an elastic. The grackle immediately pecked through the tissue paper, pulled the elastic off the box, ate all the food inside and then pushed the box over. Only after observing the grackle did a dove peck at the tissue paper, but even then it was very difficult for the dove to pierce it. The only motions towards the elastic were downward pecking movements.

Even with these differences between motor capabilities and diet, Zenaida doves still preferentially imitated both the food choice, and a food finding technique of a grackle demonstrator. Grackles roost communally (French 1973) and feed in groups, thereby exploiting unevenly distributed food sources

more efficiently according to the "information center" hypothesis (Ward and Zahavi 1973) Grackles probably also experience a greater range of food types compared to doves, as their foraging is not restricted to small areas. Therefore, by being able to observe and join foraging grackles, doves are exposed to more foraging information than they would be by observing conspecifics. However, observing a heterospecific demonstrator necessarily involves a great deal of filtering out of irrelevant information about both food and behaviour, as the doves have different digestive and motor capabilities. The added cost of filtering must thus be weighed against the lower cost of aggression and/or the higher value of foraging information to determine preferential learning from the heterospecific. Preferential interspecific learning is thus all the more surprising given these factors.

Effects of scrounging on learning

Joining the food find of a skilled individual is known to inhibit the transmission of food-finding skills in pigeons (Giraldeau and Lefebvre 1986, 1987). In this study, an experimental evaluation of this phenomenon in Zenaida doves was not possible, since observers could never share the demonstrator's food discovery. The experiments also imposed a different situation on the birds from one that would occur normally. In the field, a dove at a food patch would most probably direct aggression to a conspecific which attempted to share its food find. In the cage experiments, the dove demonstrator is prevented from doing this. However, the field study indicates that learning may not necessarily be inhibited by scrounging since the presence of grackles is not constant. Lefebvre (1986) has shown that behaviours are transmitted more in unstable populations where skilled individuals are frequently absent and Lefebvre and Palameta (1988) have demonstrated through computer simulations that instability of populations is sufficient to counteract the frequency-dependent inhibition caused by scrounging.

As a first stage in the examination of the dynamics of social learning in mixed species groups, the results revealed here are intriguing. Determining the precise conditions in which one would find inhibition of social learning following interspecific joining can only be left to future studies.

Social Learning and Scramble Competition

The evidence from the field study shows that doves use scramble competition with grackles and interference competition with conspecifics. Palameta (1989) has proposed that scramble competition may increase the selective pressures on opportunistic animals to learn novel skills. Opportunism, as Klopfer (1959) first suggested, frequently exposes animals to novel and unpredictable foods. When opportunism is combined with scramble competition, rapid ingestion of novel foods may be most efficiently achieved by social learning. Genetic pre-programming of behaviours cannot track novelty as quickly as learning can, and individual learning is slower than social learning unless extensive shaping occurs (Corson 1967, Lefebvre and Palameta MS).

Lefebvre and Palameta (1988) have proposed that group foraging may have favoured the appearance of cultural transmission, since gregarious animals most often compete by scramble techniques. The present study, combined with the results of Lefebvre and Palameta (MS), suggests that group foraging should not be restricted to monospecific cases, as implied by Lefebvre and Palameta (1988), but should include both intra- and interspecific social foraging. The important factor may not be whether foraging aggregations include one species only or several species, but the type of foraging interactions that occur within the aggregations. Interference competition may disrupt any potential social information and leave only scramble competition as both the source and selective pressure for cultural learning. The precise species one is competing with by scrambling may thus be less important than the existence of scramble competition itself.

This hypothesis is consistent both with studies on the gregarious feral pigeon and the territorial Zenaida dove. Pigeons predominantly forage with conspecifics and use scramble competition against them rather than interference. They have been shown to learn fairly easily from conspecifics in numerous studies (Epstein 1984, Palameta and Lefebvre 1985, Palameta 1989, Lefebvre and Palameta MS). In contrast, Zenaida doves use interference competition with conspecifics and scramble competition with grackles. Social learning from conspecifics has been found to be difficult both in the present study and that of Lefebvre and Palameta (MS). Indeed, as this thesis has shown, Zenaida doves prefer to learn from the heterospecific they normally compete with by scrambling in the field.

The scramble competition hypothesis can thus replace the gregarious foraging hypothesis proposed by Lefebvre and Palameta (1988). Both territorial and group-living species can be used to test predictions from the hypothesis. For instance, if scramble competition is the key factor and not the fact that one is foraging with a conspecific or a heterospecific, gregarious birds like the pigeon and the grackle should show no demonstrator preference. In Montréal, pigeons routinely encounter species like House sparrows (*Passer domesticus*) and European starlings (*Sturnus vulgaris*) when foraging with other pigeons (pers. obs.). Since scramble competition is used both intra- and interspecifically, pigeons should not selectively learn from other pigeons or from starlings and sparrows if the scramble competition hypothesis holds. In the same way, if we reverse the design used in this thesis and present grackle observers with dove and grackle demonstrators, we would also not expect significant demonstrator preference.

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Table 1

The mean number of birds present per scan and the total frequency of joining and aggressive interactions for the five species seen on provisioned trials

	Zenaida dove	Carib grackle	Lesser Antillean bullfinch	Glossy cowbird	Ground dove
Mean number of birds/scan	1.15	7.86	0.18	0.32	0.01
Joining by Zenaida doves towards	207	401	18	8	1
Aggression between Zenaida doves and	1374	17	0	0	0

Table 2

Two different methods of calculating the expected frequency of doves joining or aggressing conspecifics and grackles at three hypothetical patches of food based on a frequency of 200 observed events

Method	Composition of patches	Relative proportions	Expected frequencies
<u>Example 1</u>			
Number of birds present	A 1 dove B 15 grackles C 3 grackles	1 dove = 0.05 18 grackles = 0.95	intraspecific = 10 interspecific = 190
Species present	A dove (n=1) B grackles (n=15) C grackles (n=3)	1 patch with dove = 0.33 2 patches with grackles = 0.66	intraspecific = 67 interspecific = 133
<u>Example 2</u>			
Number of birds present	A 1 dove, 1 grackle B 14 grackles C 3 grackles	1 dove = 0.05 18 grackles = 0.95	intraspecific = 10 interspecific = 190
Species present	A: dove (n=1) grackle (n=1) B grackles (n=14) C grackles (n=3)	0.5 patch with dove = 0.17 2.5 patches with grackles = 0.83	intraspecific = 34 interspecific = 166

Table 3

The mean number of birds present per scan and the total frequency of joining and aggressive interactions for the five species seen on unprovisioned trials

	Zenaida dove	Carib grackle	Lesser Antillean bullfinch	Glossy cowbird	Ground dove
Mean number of birds/scan	3.64	2.57	0.48	0.02	0.32
Joining by Zenaida doves towards	123	81	11	1	3
Aggression between Zenaida doves and	468	10	0	0	0

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(* : $p < 0.05$, ** : $p < 0.01$, *** : $p < 0.001$)

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A Intraspecific, B Interspecific

(* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

Figure 20 : Total frequency of observed aggression per site, compared to the expected frequencies based on the number of birds present

A Intraspecific, B Interspecific

(* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$)

Figure 21 Schematic view of the aviary with the two experimental compartments, each compartment contains two doves waiting to be tested and one dove placed in front of its conspecific and heterospecific demonstrators

(D= Dove, G = Grackle)

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Figure 1

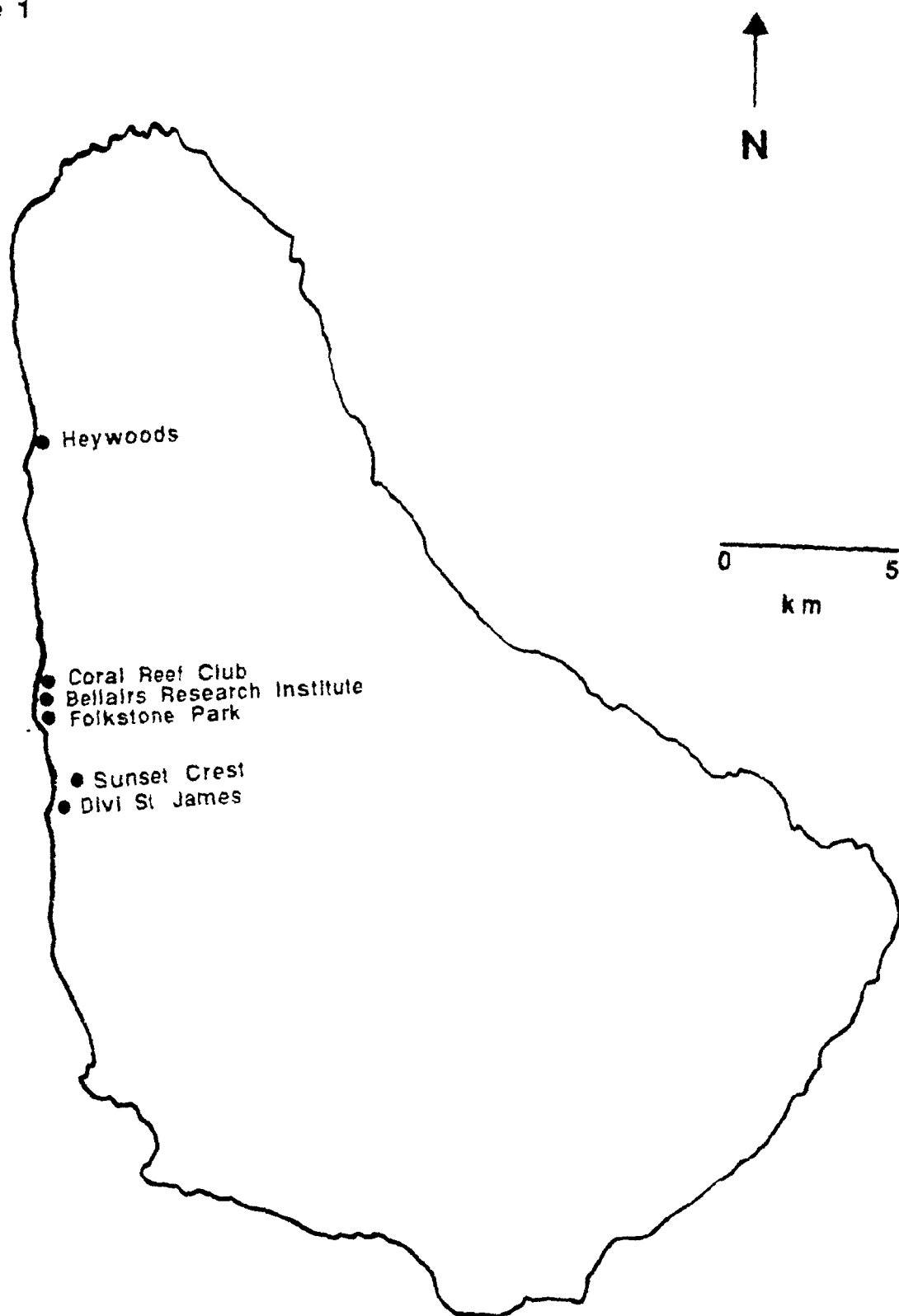


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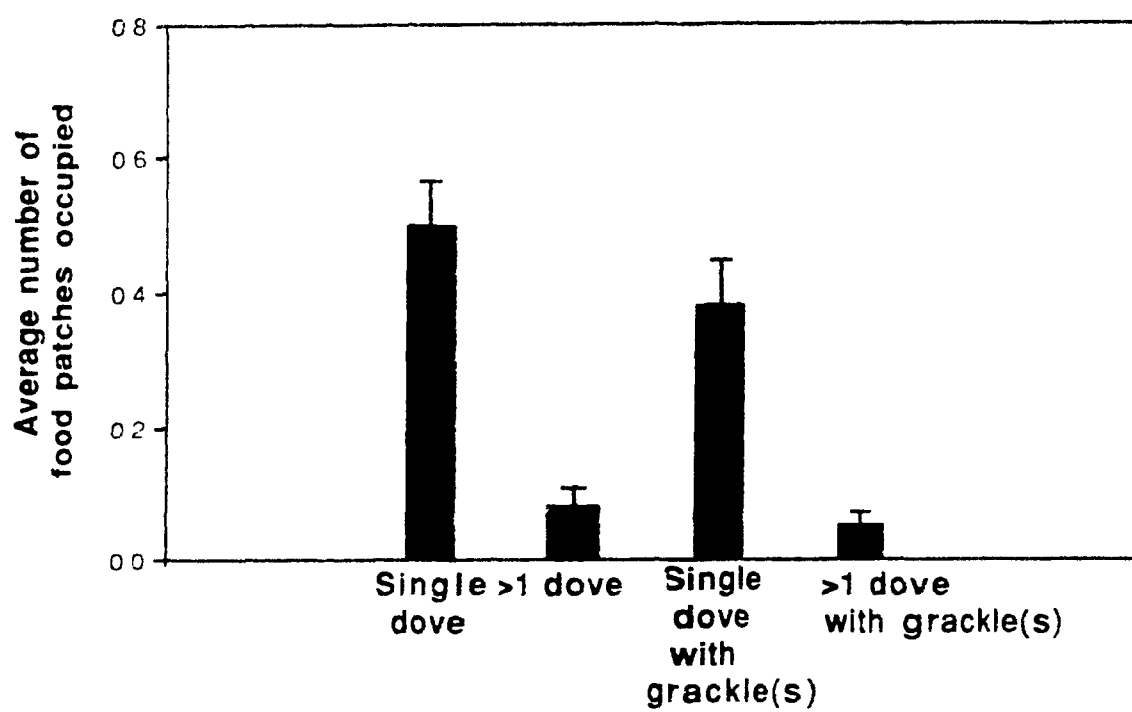


Figure 3

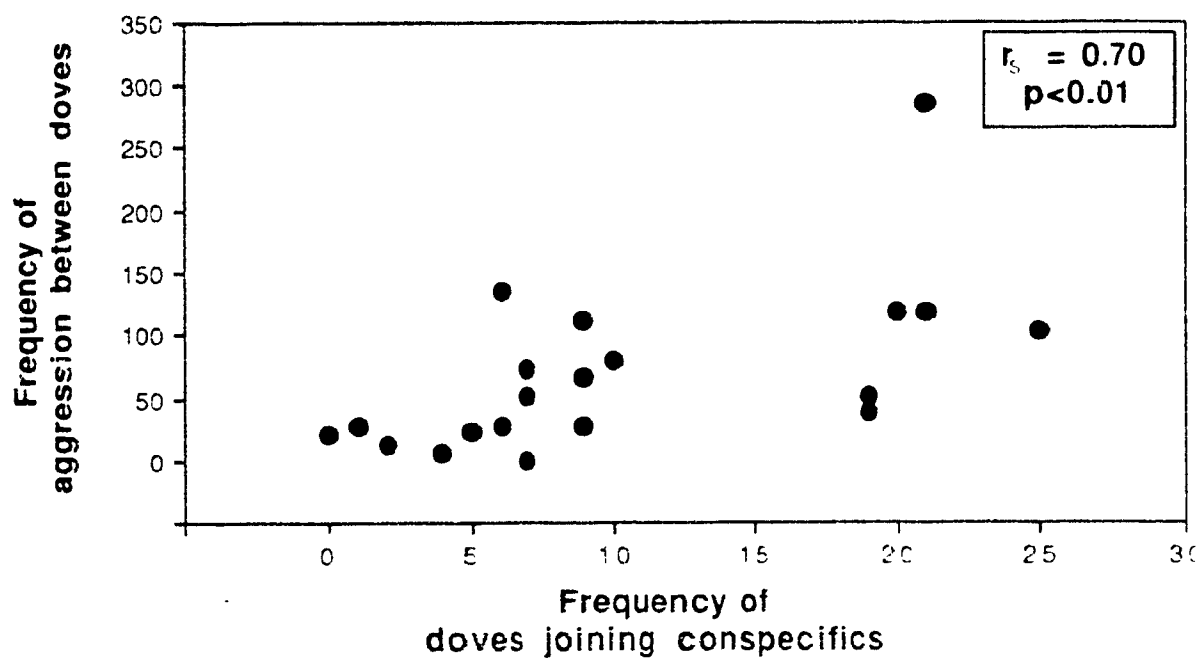


Figure 4

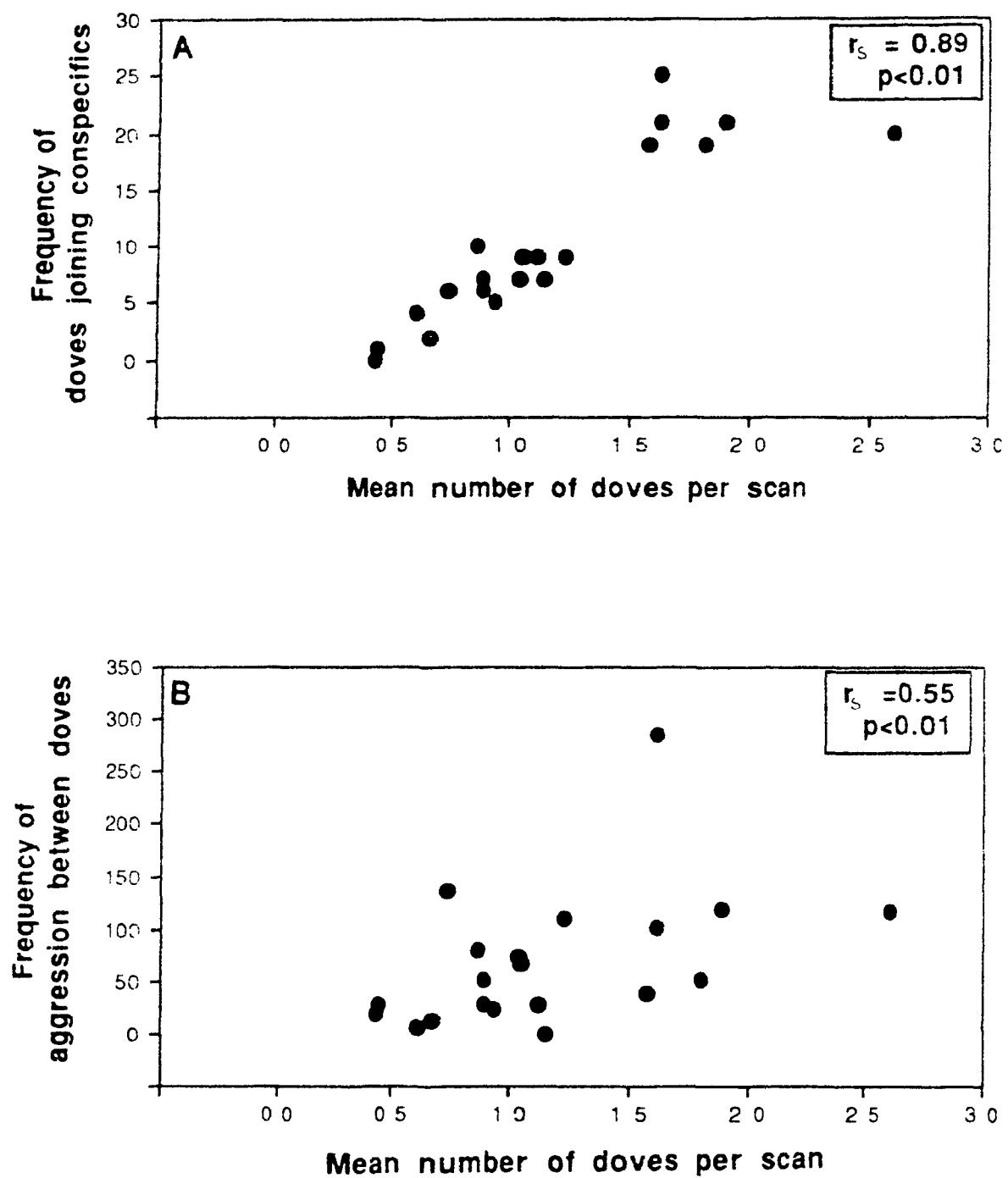


Figure 5

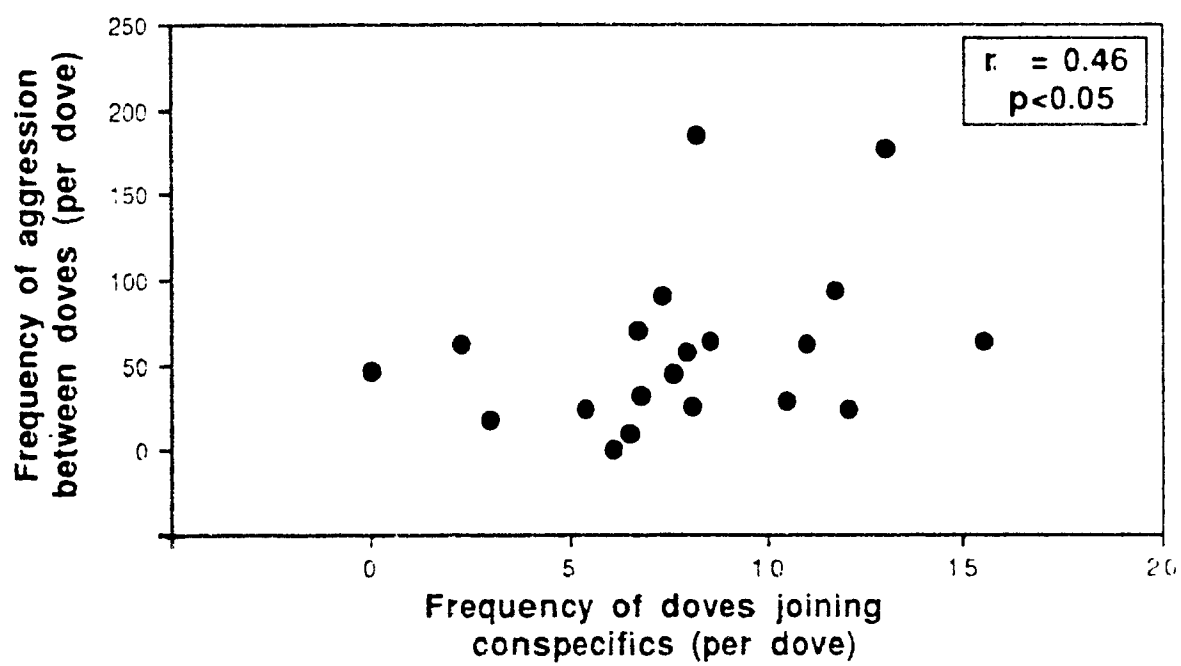


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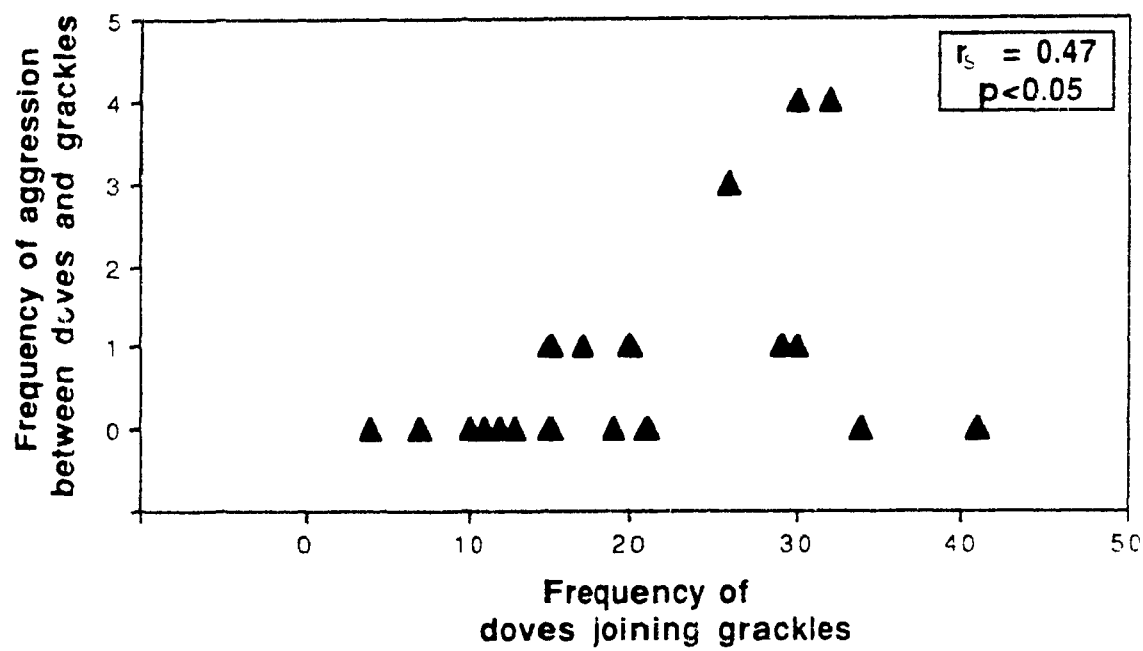


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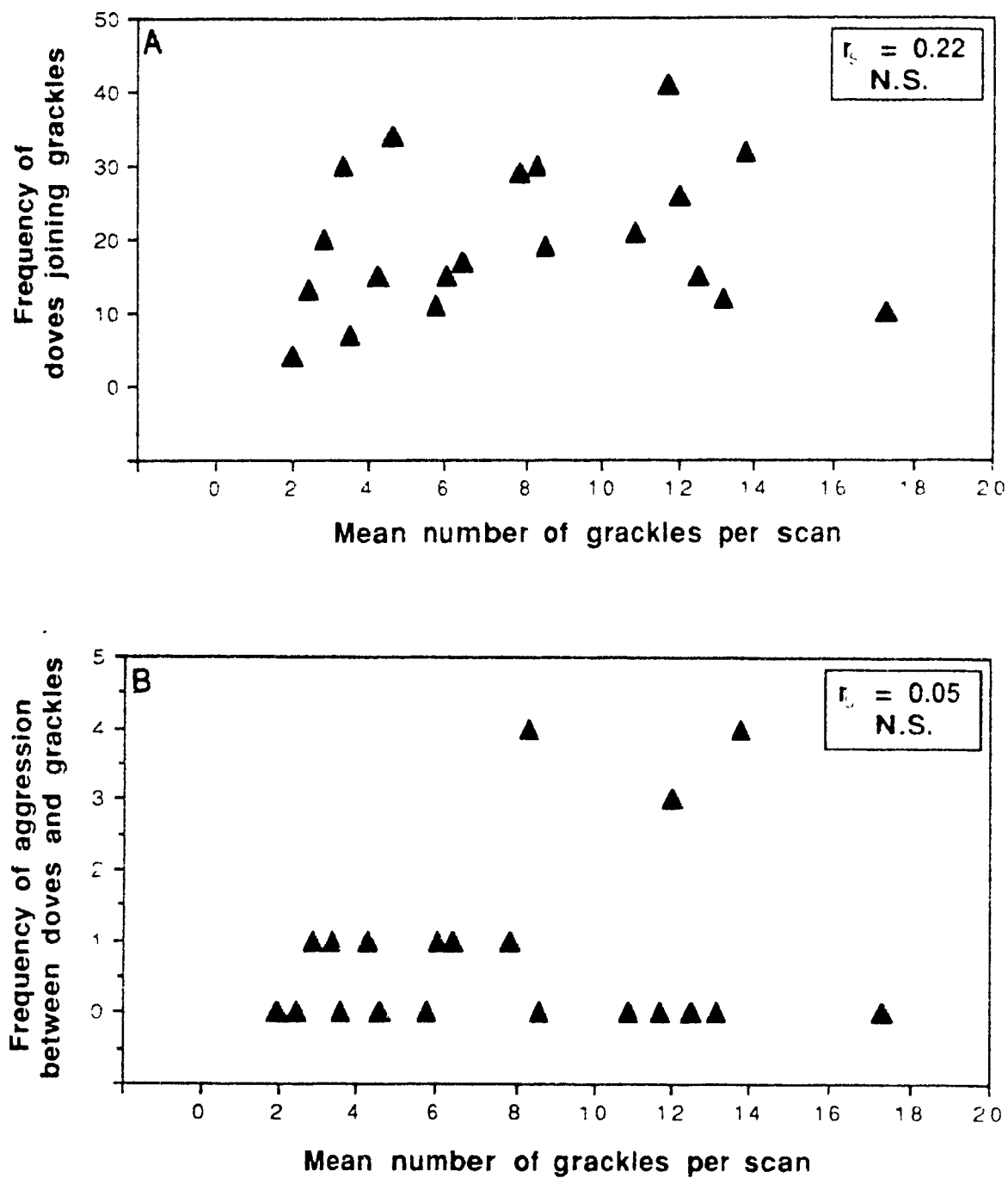


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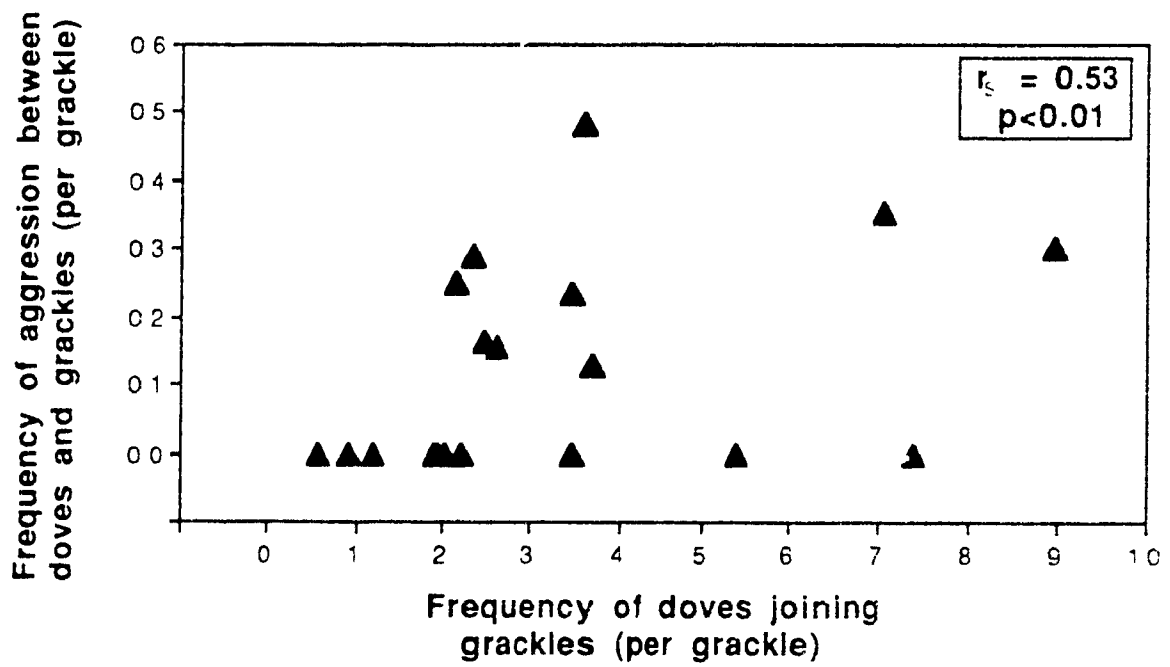


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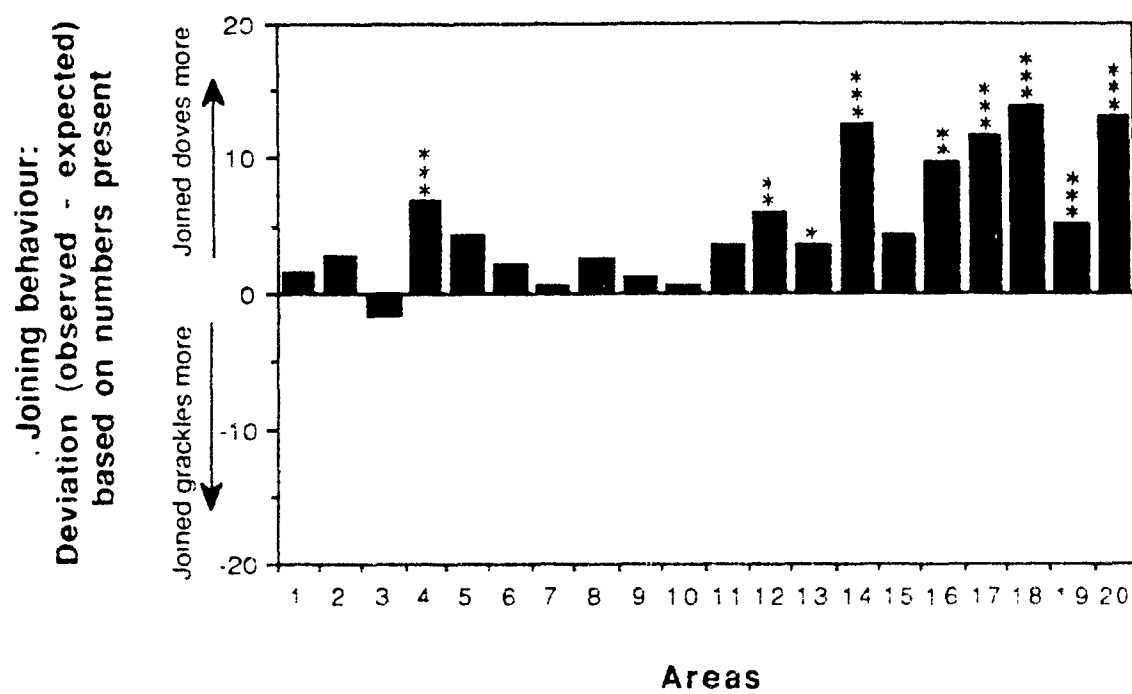


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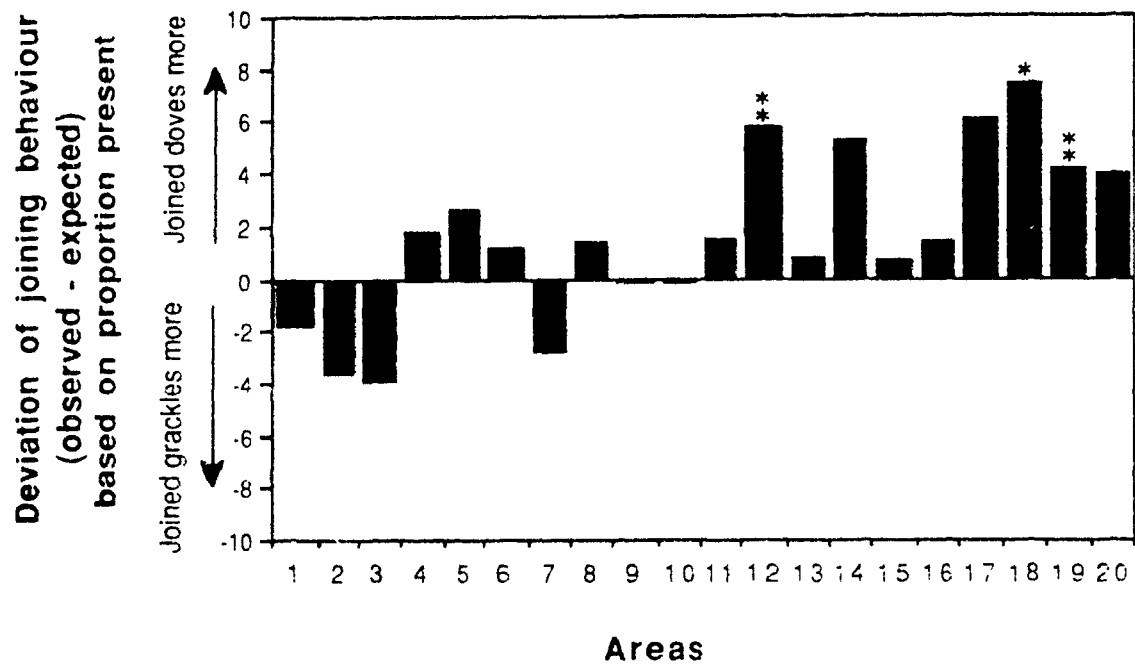


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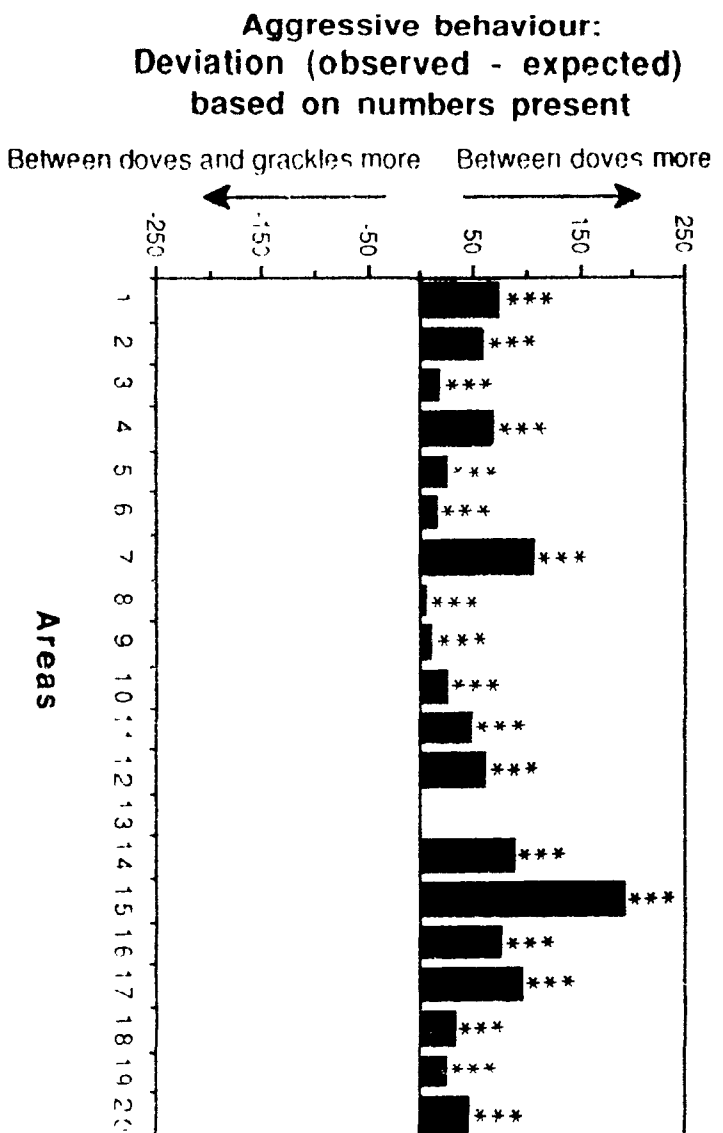


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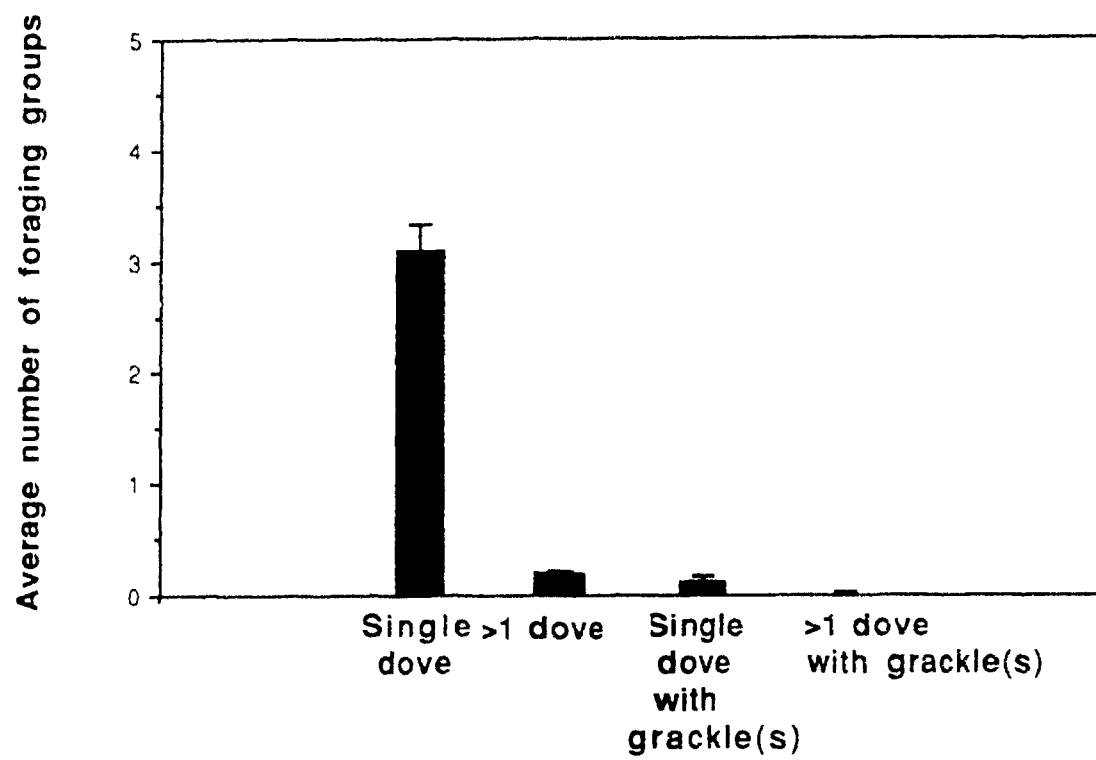


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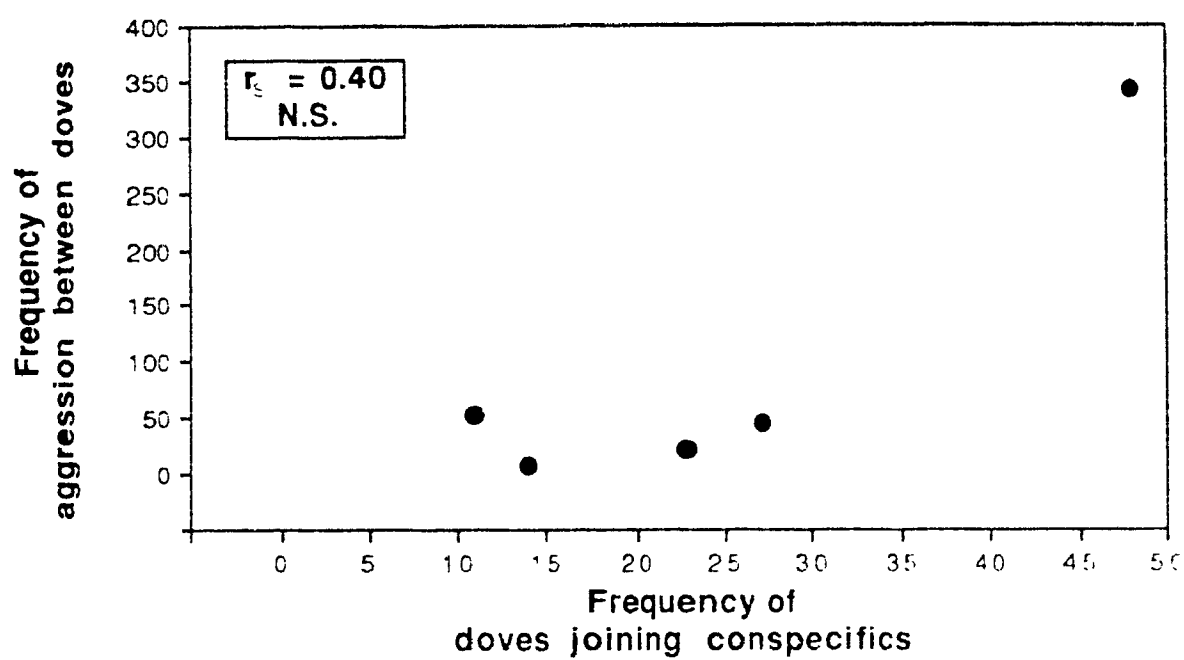


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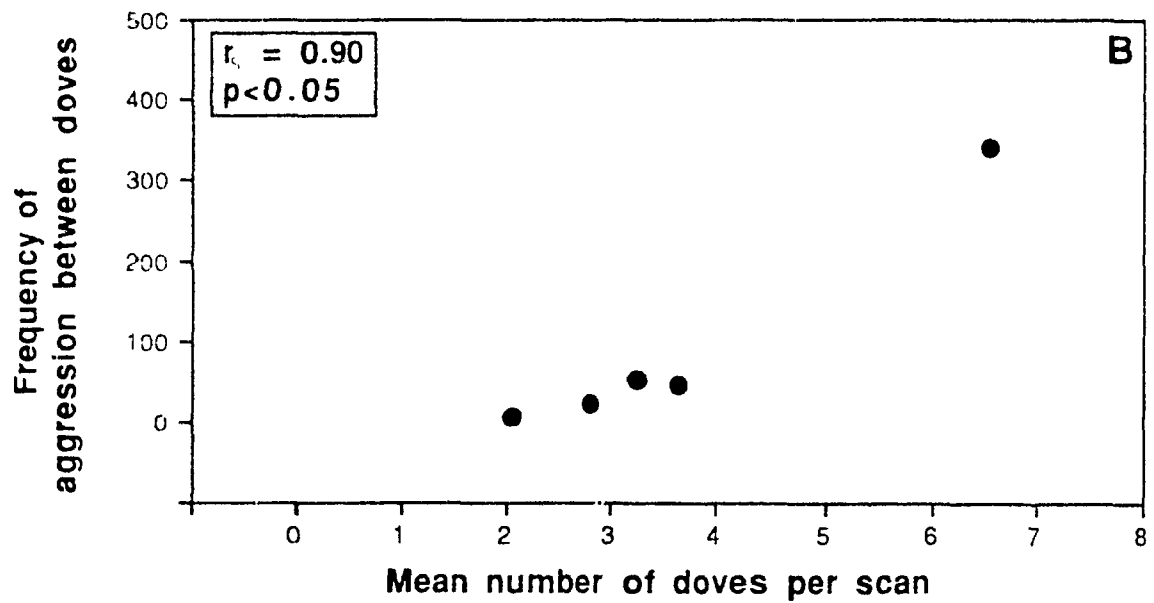
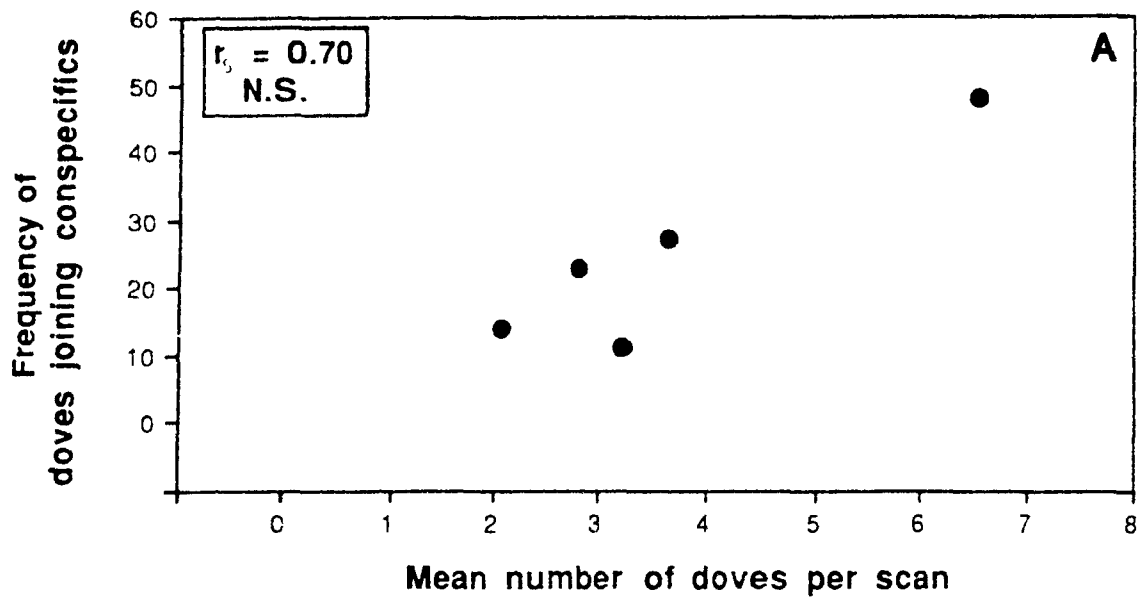


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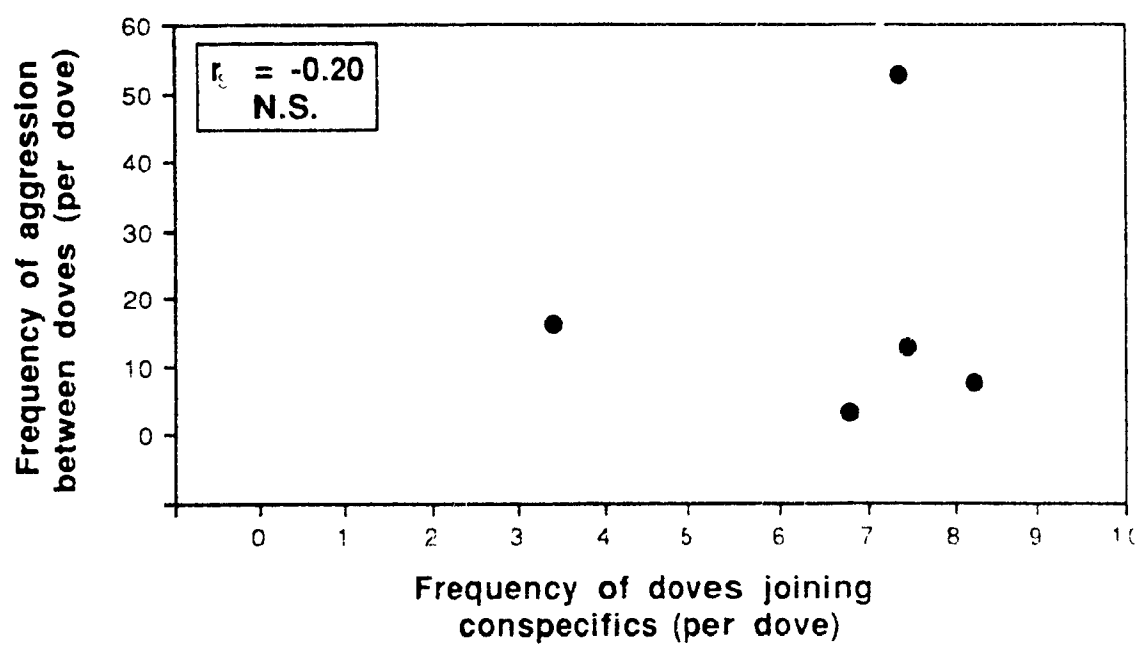


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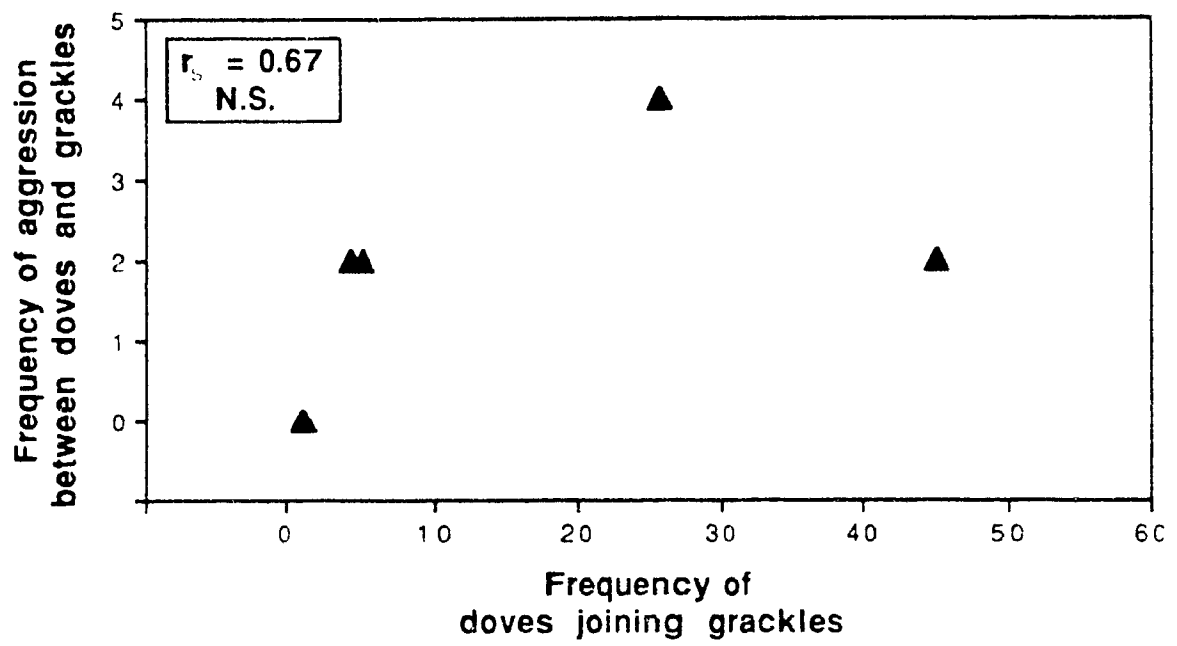


Figure 17

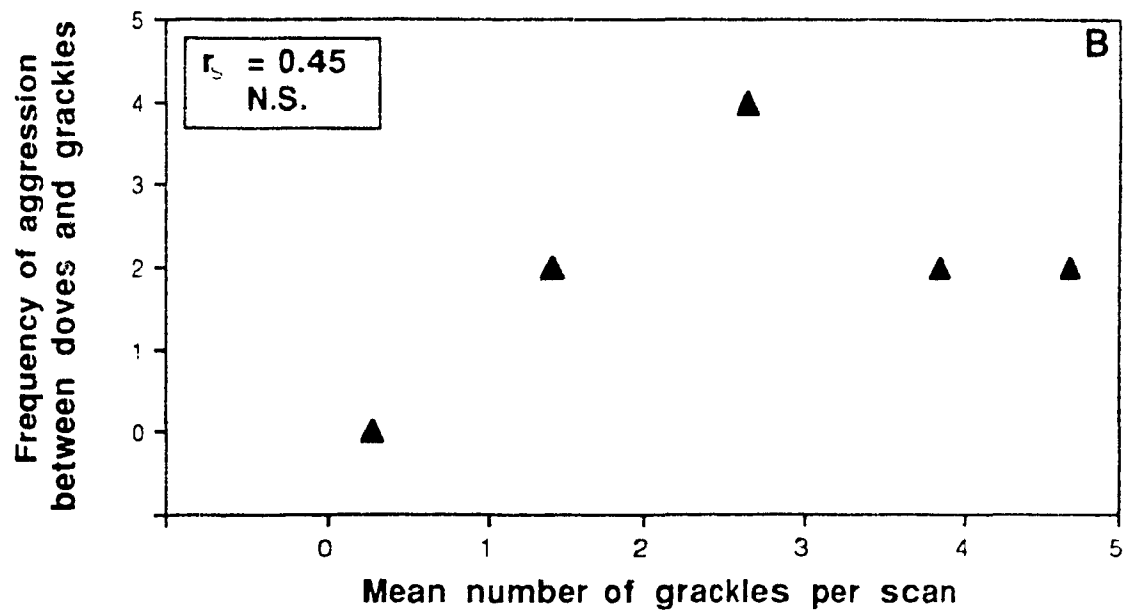
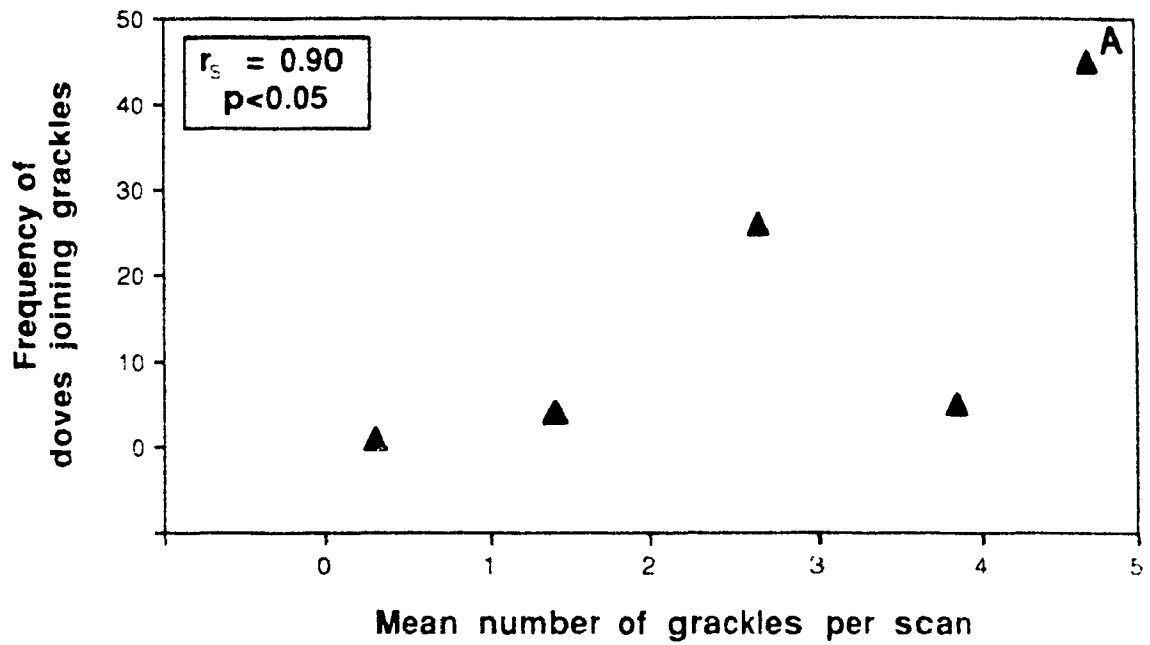


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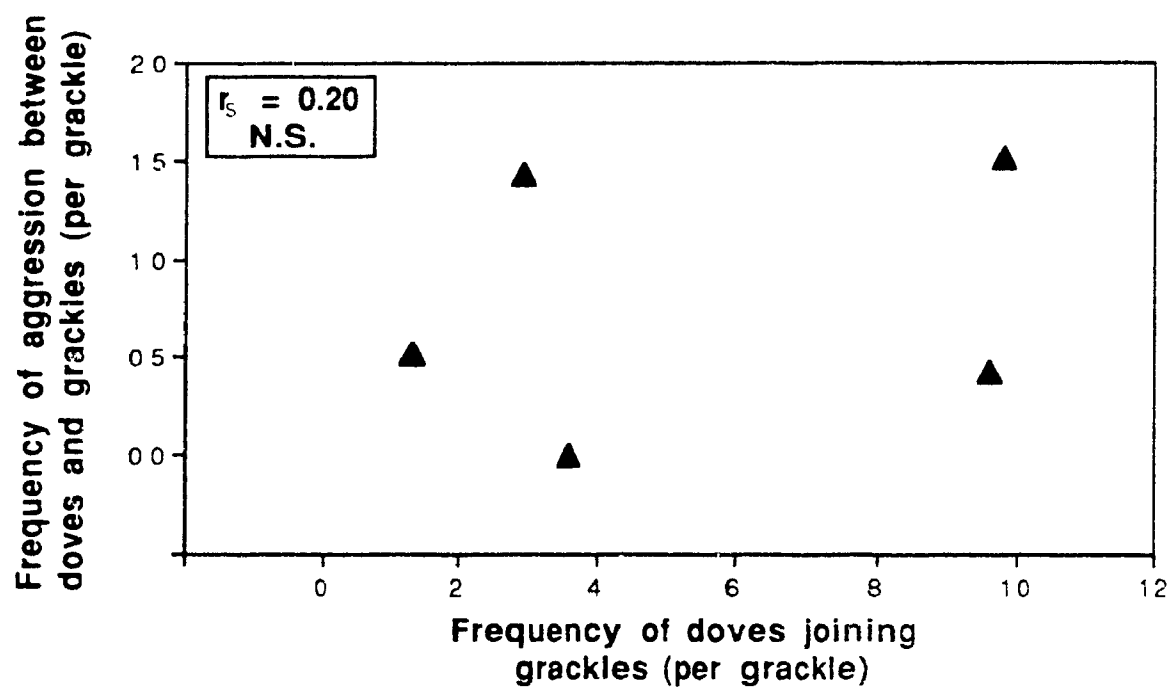


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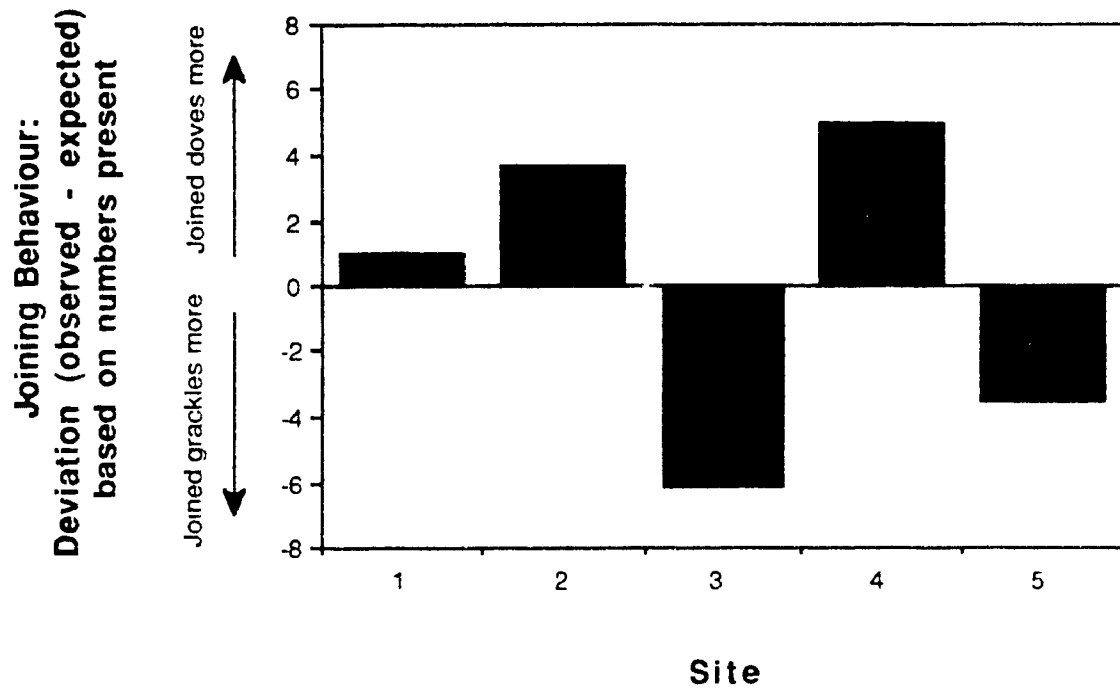


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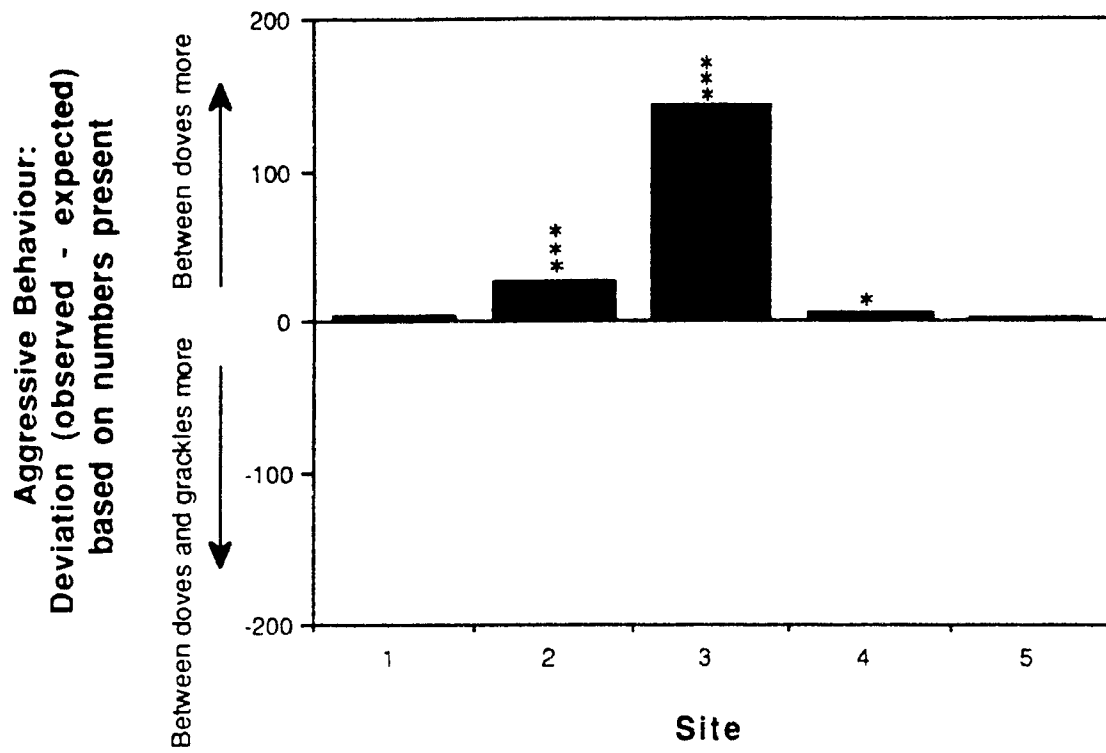


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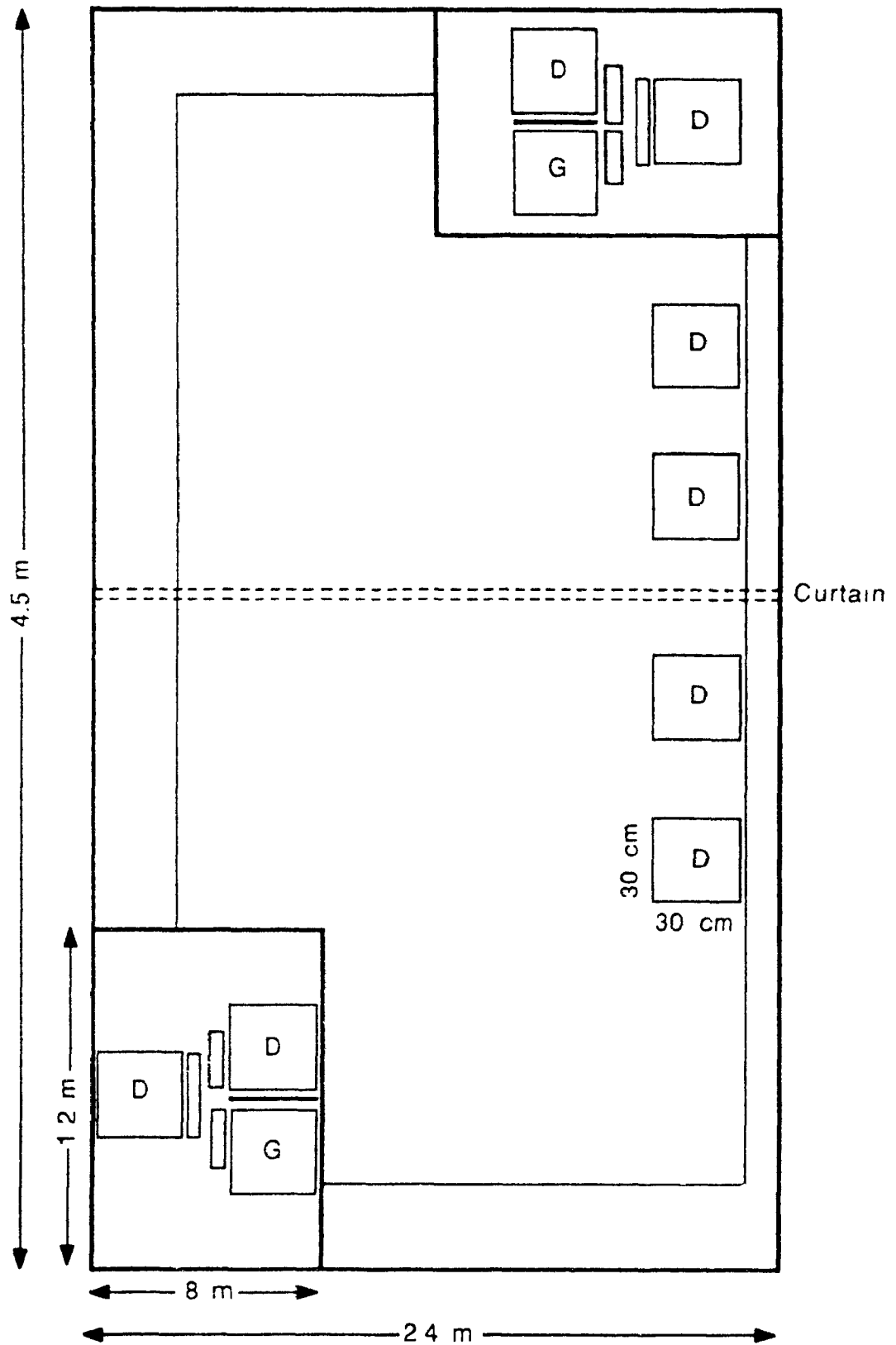
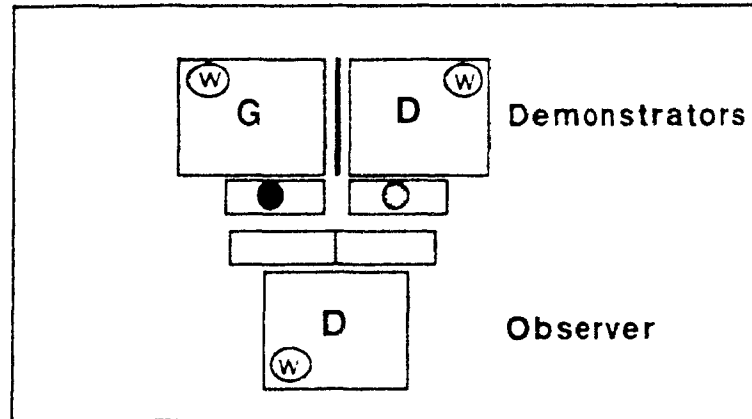
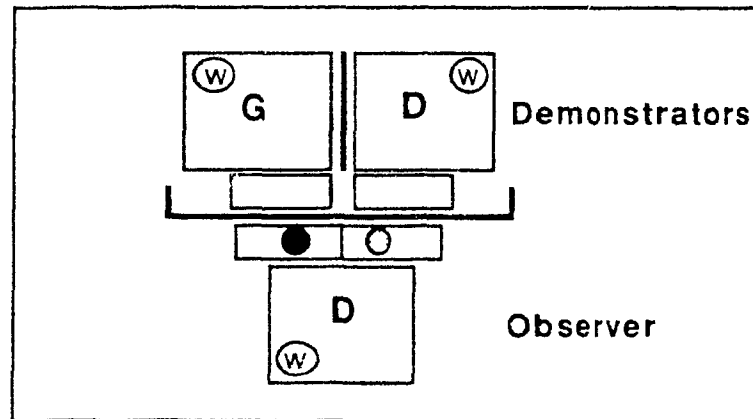


Figure 22



Demonstration



Choice Test

Legend	
w	- water
D	- Zenaida dove
G	- Carib grackle
●	- red rice
○	- green rice
┌	- wooden partition

Figure 23

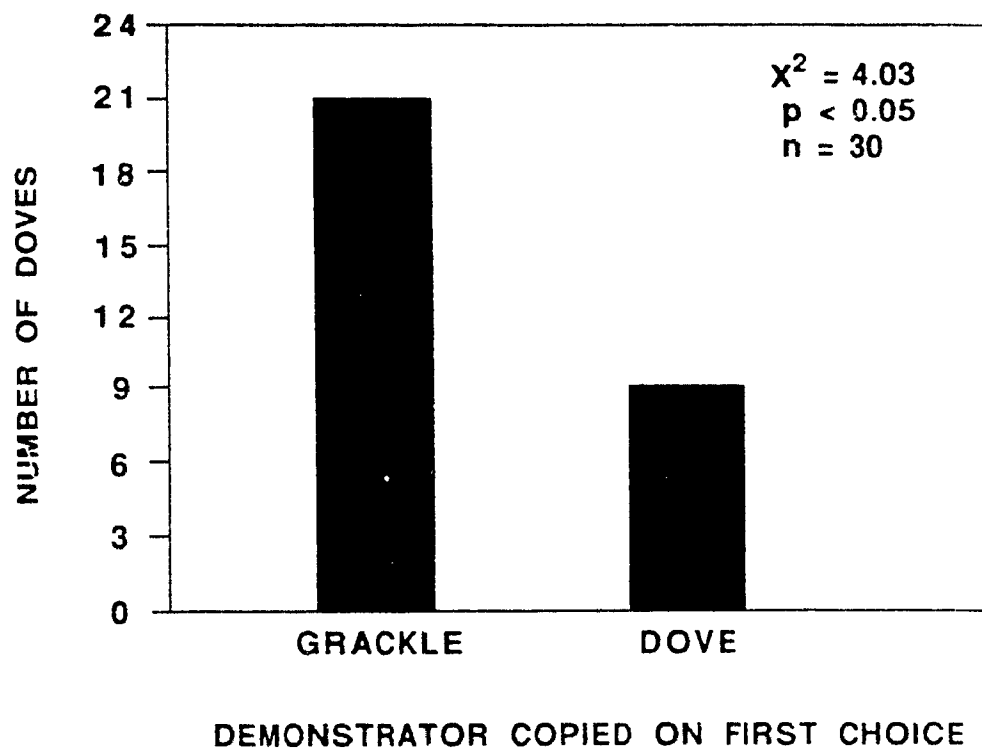


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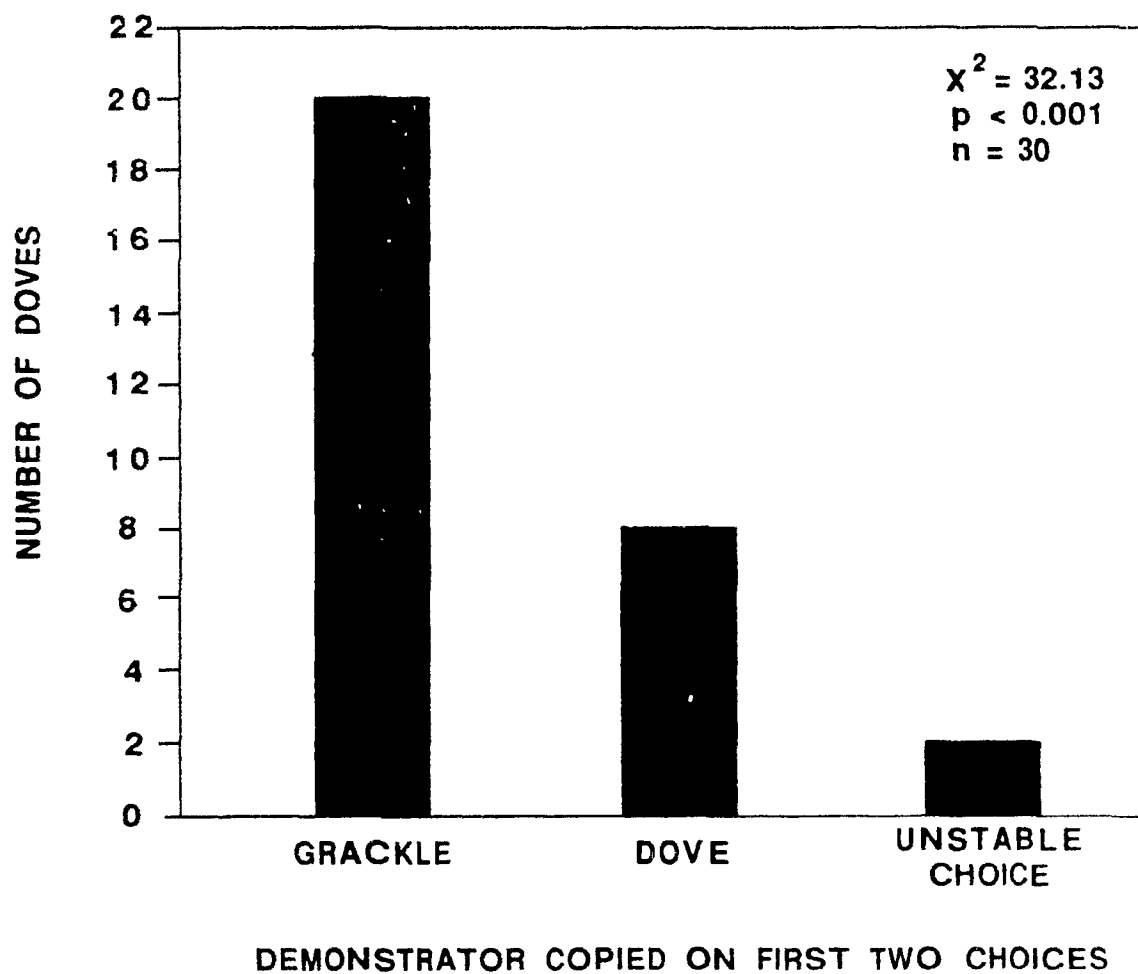


Figure 25

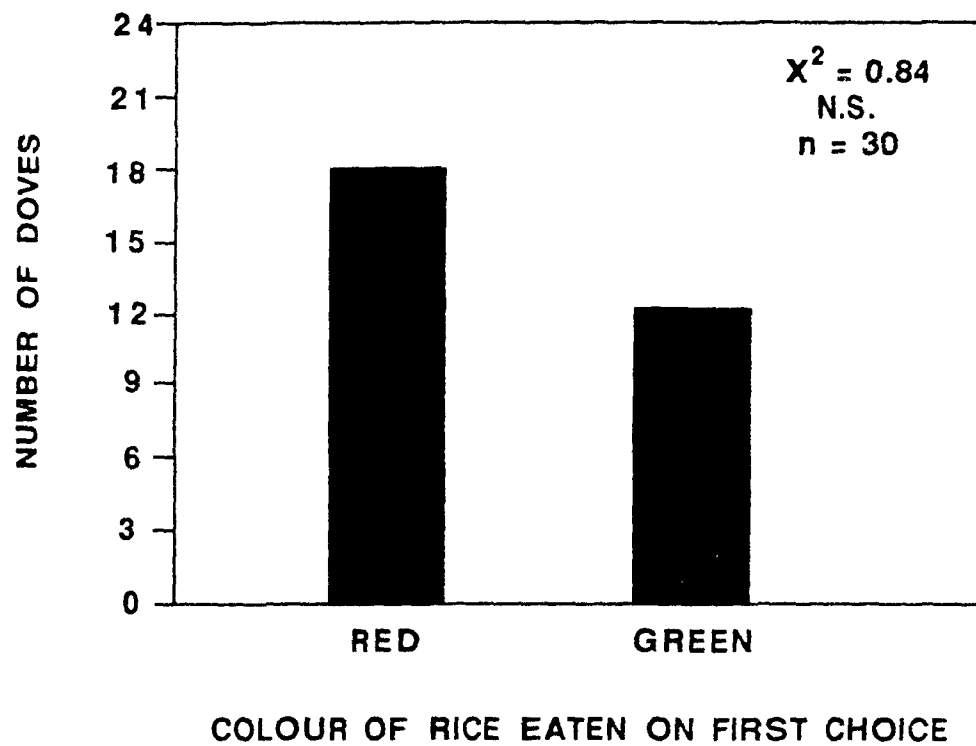
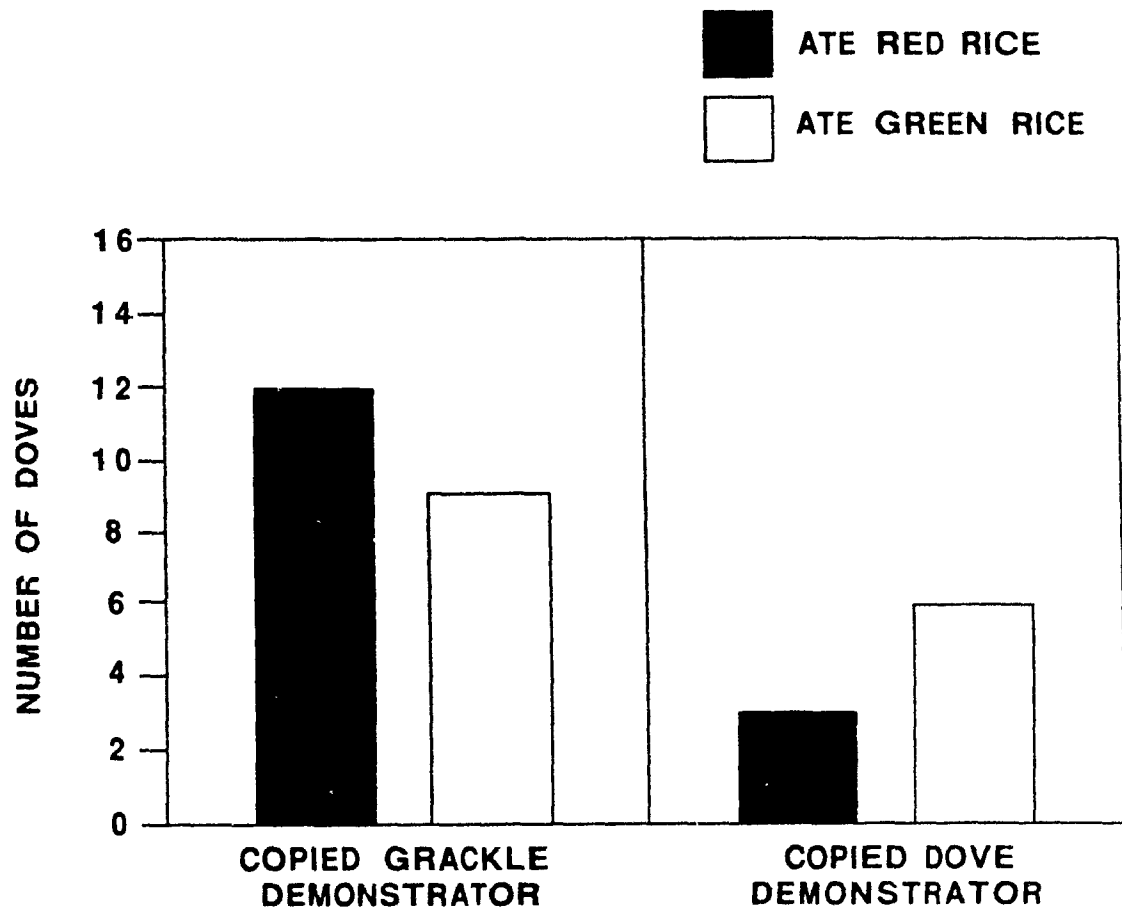
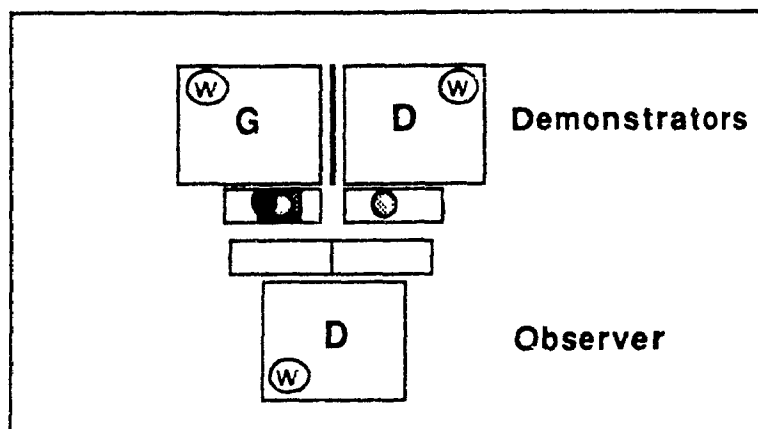


Figure 26

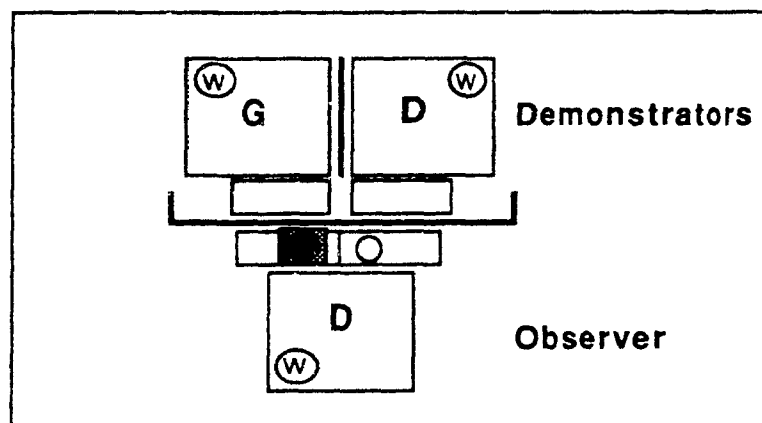


$\chi^2_c = 0.63$
N.S.
 $n = 30$

Figure 27



Demonstration



Choice Test

Legend

- w - water
- D - Zenaida dove
- G - Carib grackle
- - petri dish with food
- - empty petri dish
- ◐ - box with lid removed
- ◑ - box with lid covering food
- - wooden partition

Figure 28

