ACQUISITION OF FORAGING SKILLS IN JUVENILE RINGDOVES: WHO DO THEY LEARN FROM?

by

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ABSTRACT

Post-fledging parent-offspring associations are observed in many species of birds. One suggested function of this association is for juveniles to learn about foraging by observing their parents. In gregarious species, however, juveniles also encounter other unrelated adults and can potentially learn foraging skills from non-kin. This thesis seeks to determine if juvenile birds preferentially select foraging information from their parents, by examining the acquisition of novel food-finding skills in juveniles of a flock-feeding species - the ringdove (*Streptopelia risoria*).

This study consisted of four experiments. The first experiment examined the flock feeding behaviour of juvenile ringdoves foraging in a small aviary flock composed of kin and non-kin; frequencies of local enhancement, food begging and aggression were recorded, as well as the individuals that the juveniles associated with while searching for food. The aviary study showed that juvenile ringdoves foraged significantly more often with their kin and were aggressed more by non-kin. The last three experiments tested juveniles on three components of foraging; novel food type, environmental colour cues associated with food and novel food-searching techniques. All three involved a choice-test where the juveniles had their father and an unrelated flock member as demonstrators providing different, but equally appropriate, information about each situation. All three choice-tests showed there was no preference for selecting either demonstrator's solution. Taken together, the results of these four experiments suggest that juvenile doves in the field may appear to learn from their parents simply because they associate more with them, but that there is no preference for the specific information provided by the parent when an equally relevant solution is provided by an unrelated demonstrator.

RESUME

Les associations entre parents et oisillons après que ceux-ci aient quitté le nid sont observées dans un grand nombre d'espèces d'oiseaux. En s'associant à leurs parents, les jeunes apprennent peut-êcre à chercher leur nourriture par le biais de l'imitation. Chez certaines espèces grégaires cependant, les jeunes peuvent aussi observer d'autres adultes que leurs parents. Ces adultes non-apparentés peuvent eux aussi servir de sources d'information alimentaire. Cette thèse essaie de determiner si les oisitions préfèrent l'information fournie par leur parents à celle fournie par ces congénères non-apparentés. L'espèce étudiée est la tourterelle à collier (*Streptopelia risoria*).

Le t'avail comporte quatre expériences. Dans la première, le comportement de juveniles qui cherchent de la nourriture en compagnie de tourterelles apparentées et non-apparentés a été observé dans une voltère. Les fréquences d'agression, d'accentuation locale et de sollicitation de nourriture ont été systématiquement notés, ainsi que les individus avec qui les juveniles se sont associés lors de leur quête de nourriture. L'étude en volière a démontré que les juveniles cherchaient plus fréquemment leur nourriture en compagnie de leurs parents et qu'ils étaient plus souvent agressés par les adultes non-apparentés. Les trois dernières expériences ont examiné trois aspects de la recherche de nourriture des juveniles: l'apprentissage de nouveaux types de nourriture, l'apprentissage d'indices du milieu associés à la nourriture, ainsi que l'apprentissage de nouvelles techniques de recherche. Dans chacune de ces expériences, les juveniles devaient choisir entre une solution fournie par le parent et une solution fournie par l'individu non-apparenté. Les expériences n'ont démontré aucune préférence pour l'un ou l'autre des deux types de démonstrateurs. Les résultats de ces quatre expériences suggèrent que les tourterelles apprennent plus souvent de leurs parents parce qu'ils s'associent plus fréquemment avec eux. Si un démonstrateur non-apparenté montre une technique aussi appropriée pour résoudre un problème alimentaire, la jeune tourterelle ne montre cependant aucune préférence pour l'un ou l'autre des deux démonstrateurs.

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GENERAL INTRODUCTION

In many avian species, juveniles continue to associate with their parents after leaving the nest. Several functions have been proposed for this association. One suggested function is the social learning of foraging behaviour by offspring observing their parents, a possibility which is examined in this thesis.

Post-Fledging Parental Care

Post-fledging associations between parent and offspring are known to occur in several bird species. However, because of the difficulty in detecting and following juveniles during this stage of their development, studies often provide little detail on the post-fledging period. Those studies that do provide systematic observations include reports on eagles (Walker, 1987; Alonso *et al.*, 1987), kingbirds (Morehouse & Brewer, 1968), oystercatchers (Norton-Griffiths, 1969), mourning doves (Hitchcock & Mirarchi, 1984 & 1986) and several species of passerines (Davies, 1976; Smith, 1978; Hötker, 1982; Moreno, 1984).

Despite the fact that offspring have left the nest and acquired some degree of locomotor independance, parents often continue to care for the young after fledging. The duration of the post-fledging care period varies considerably between species. From the limited number of quantitative studies available, it appears that post-fledging parental care of altricial birds can encompass approximately half the total duration of parental care of hatched young. This ranges from two to three weeks in passerines and columbids to several months in frigatebirds or terns. During this time, parents continue to feed their young but progressively decrease the amount of food given as the young grow older and begin to forage on their own. This has been observed in kingbirds (Morehouse & Brewer, 1968), spotted flycatchers (Davies, 1976), and mourning doves (Hitchcock & Mirarchi, 1984).

Once the young begin foraging for themselves, they are usually more inefficient than adults. Often juveniles are seen to peck at inappropriate objects before succeeding in obtaining food for themselves, as reported in spotted flycatchers (Davies, 1976), song sparrows (Smith, 1978), wheatears (Moreno, 1984) and in mourning doves (Hitchcock & Mirarchi, 1984). Buckley and Buckley (1974) also found that juvenile royal terns were inefficient foragers: although they had the same prey capture

success rate as adults, they only made half as many dives per unit time and spent twice as long foraging. Juvenilos also tended to drop caught prey more often than adults.

Alternatively, juvenile birds may eat food which is easier to find or to handle than the food adults eat. For example, juvenile kingbirds start foraging on fruit and invertebrates found on branches even though flying insects are the main staple of adult kingbirds (Morehouse & Brewer, 1968). Juvenile starlings forage on cherries until they are able to forage efficiently on the invertebrates their parents feed on (Stevens, 1985).

In part, juveniles are unable to fend for themselves because they leave the nest before they are fully grown; their wings are still short and their muscles are not fully developed so they can only fly short distances. In kingbirds (Morehouse & Brewer, 1968), passerines (Davies, 1976; Smith, 1978; Moreno, 1984) and columbids (Hitchcock & Mirarchi, 1984) the fledged young remain virtually motionless during the first days after leaving the nest. Their flying ability gradually improves over the course of the post-fledging period. In those species that require flight for foraging (e.g. raptors, marine birds or flycatching birds), juveniles can only begin to forage on their own once they have mastered flying. In the interim, parents must continue feeding them. This occurs, for example, in golden eagles. Walker (1987) found that prior to 8 days out of the nest, the juvenile golden eagle could fly no more than 25 m. By day 12, they could fly up to 50 ni. After 14 days, juveniles began to lead flights accompanied by their father. It was only when they were 25 days post-fledging that they could fly well, but they still remained within the nest valley (approximately 6 km² compared to the parents home range of c. 49 km²) until they were 6 weeks post-fledging. Until they were able to fly and thus capture their own prey, juveniles were seen pouncing on heather stalks and prey remains brought by the father.

For frigatebirds, since the majority of food is obtained either in the air or by skimming over the sea or ground without landing, juveniles must learn how to fly accurately before they can forage for themselves (Stonehouse & Stonehouse, 1963). Thus juveniles remain dependent on their parents for food until they begin to fly at seven to eight months of age; they continue to remain at least partly dependent for a further three to four months after learning to fly.

Not only are the wings and muscles not fully developed at fledging but neither is the beak, so that many juvenile birds are unable to forage efficiently until their beaks are more mature. Foraging ability thus also improves gradually as the beak develops. For example, Stevens (1985) found leatherjackets to be the most important food for starlings in the area studied and made up 82% of the adults diet, but only 35% of the juveniles' diet. It is found that starlings gradually became more skillful at capturing leatherjackets and his skill was correlated with growth of the bill (see Marchetti & Price (1989) for an extensive review of the developmental contraints which affect juvenile foraging abilities). Thus, one function of post-fledging parental care is for the parents to supplement the juveniles own foraging efforts until the juveniles have completed most of their growth.

Upon fledging, not only must juveniles learn to forage for themselves, but they must also learn how to recognize and avoid predators. Often, this stage exhibits a high mortality rate. Sullivan (1989) found that the main cause of death in nestling and fledgling juncos was predation. According to Johnston (1982), post-fledging parental care may have evolved in many species to reduce this mortality rate. In addition to feeding their young, the parents can also offer protection - by warning them of potential danger. Since invenile flight structures and anti-predator behaviours are poorly developed at fledging, parents may have to compensate for this deficiency by increased vigilance and specialized behaviours designed to lead predators away from their young. Walker (1987) believes that the golden eagle father flies with its offspring in order to protect it, since the father was observed chasing off mobbing crows while its offspring flew to safety. In yellow-eyed juncos, recently fledged young do not seem to actively look out for predators since their scanning rates were found to be very low. Sullivan (1988) found that the parents were even more vigilant during this time by increasing their own scanning rate. In ostriches, Sauer & Sauer (1965) found that although parents with fledglings usually avoided encounters with local predators by quietly running away, when this was not possible, the parent would perform an elaborate distraction display to attract the predator away from the well camouflaged young.

Thus, evidence suggests two important functions for post-fledging care: 1) to supplement feeding until juveniles are capable of foraging for themselves and 2) to offer protection against predators. In addition, parent-offspring associations may allow juveniles to learn from their parents which foods to eat or avoid, which cues in the environment should be associated with food, and what searching and handling techniques should be used to obtain food.

Social Learning Approaches

When the acquisition of novel behaviours by individuals is somehow influenced by interactions with other individuals, it is commonly referred to as social learning. In contrast to genetic transmission of behaviour, both social and individual learning allow an individual to rapidly adapt to changes in the environment. Social learning is less risky and less time consuming if individuals can learn about particular food sources by watching other knowledgeable individuals at these sources (Galef, 1976). The process by which these newly acquired behaviours are spread throughout a population is called cultural transmission.

Social learning can be divided into three categories depending on the amount of social influence needed for a novel behaviour to be learned (Thorpe, 1963). These categories are social facilitation, stimulus enhancement and imitation. Social facilitation occurs when an individual performs a behaviour it already knows after it sees other individuals performing the same behaviour (Clayton, 1978). While, strictly speaking, it does not involve learning, it can lead to learning if the behaviour is performed in a novel context. Stimulus enhancement is when an observer's attention is drawn to a particular stimulus or to its location (in the latter case, it is called local enhancement) because of another individual's interaction with that stimulus. The correct response is subsequently learned by the observer through trial and error.

Imitation is when an individual learns a novel act by directly copying the precise novel motor act performed by another individual. Few studies have successfully demonstrated the existence of this form of social learning, which is the most cognitively complex. In fact, in most field cases, although it seems clear that the acquisition of a novel behaviour has been socially influenced, the exact form of social learning cannot be pin-pointed. In part, many of the problems have been due to conflicting definitions and terminology used in the study of social learning (see Galef, 1988 for a historical review). Other difficulties can be attributed to the inherent nature of the three main approaches used to study social learning: field observations, laboratory experiments and mathematical models.

In birds, the classic example of cultural transmission in the field is milk-bottle opening in British tits (Fisher & Hinde, 1949; Hinde & Fisher, 1951). Milk-bottle opening was probably learned independently by several birds, but within a few years the behaviour had spread throughout the tit population of England. The behaviour was believed to spread by social learning. Unfortunately, despite the large number of putative cases of social learning reported in the field, most of these reports have been anecdotal and speculative (see Lefebvre & Palameta, 1988, for a review).

In the field, social learning is very difficult to demonstrate unequivocally since it is virtually impossible to control for other forms of learning which may lead to the same result. The only way to properly test for imitation is to conduct controlled experiments in the laboratory. For bottle-opening, Sherry & Galef (1984, 1990) did this by examining a laboratory equivalent of the behaviour in chickadees, a North American relative of British tits). Although Sherry & Galef found that naive chickadees were able to learn to open by watching conspecifics do so, their results failed to prove imitation since opening could be explained by simpler mechanisms. One alternative explanation was natural shaping, given that chickadees which ate from a pre-opened version of the apparatus but saw no demonstration of the technique also learned. Many other laboratory studies have also failed to identify the process of transmission of novel behaviours, either because of a lack of appropriate controls or the use of a novel task that was too easily learned, (for reviews of these studies see Whiten, 1990; Visalberghi & Fragasey, 1990; Palameta, 1989; Galef, 1976 & 1988 and Box, 1984).

Although imitation can only be demonstrated through laboratory experiments, it is important that these studies be ecologically appropriate. A behaviour acquired in the lab must be one that could potentially occur in the wild and where appropriate opportunities exist for that species to culturally transmit that behaviour. A series of experiments by Lefebvre and Palameta has successfully demonstrated that novel foraging techniques can be culturally transmitted in feral pigeon populations and that imitation does occur in pigeons. In the lab, Palameta and Lefebvre (1985) demonstrated that naive observer pigeons could learn to pierce paper in order to obtain food by watching demonstrator pigeons. They showed that the amount of information available to the observer pigeon affected its learning rate, in that those observers who saw demonstrators pierce the paper and subsequently eat learned faster than those who only saw the demonstrator eat from a previously opened hole in the paper. Lefebvre (1986) brought this experiment into the field to show that the paper-piercing skill could spread through a wild population of pigeons. Palameta (1989) convincingly demonstrated that novel skills could be learned by pigeons through the imitation of precise motor acts of conspecifics. His experiments were carefully designed to control for other forms of learning, and his results eliminated stimulus enhancement among other things as possible explanations.

A third method of studying cultural transmission is through mathematical models, which predict how behaviours can spread through populations and what conditions are needed for transmission. These models are theoretical and for the most part their assumptions and subsequent results have yet to be empirically tested. However, in these models, the main transmission route of learned behaviours is thought to be through parent-offspring interactions (Cavalli-Sforza & Feldman, 1981; Pulliam, 1983).

Evidence for Offspring Learning from their Parents

Social learning provides a rapid means of acquiring many of the skills needed for survival. It would be particularly important to naive young, especially those of opportunistic species, whose diet is varied and changes with the availability of different food types in the environment. It is important to learn what food is present, where to find it and how to capture it; juveniles must also learn what potential food should be avoided. In the latter case, trial and error learning can be costly to naive juveniles in terms of consuming either noxious or nutrient-poor food. Post-fledging care by the parents provides juveniles with, among other things, the opportunity of learning about foraging from this association. Yet, despite the advantages of social learning and the frequent observations of juveniles and even fewer have examined whether offspring are learning by observing their parents. One such study is by Van Lawick-Goodall (1973), who found that wild juvenile chimpanzees learn how to fish for termites by watching their mothers do so before they themselves practise using a stick.

One of the best studies of parent-offspring social learning is Norton-Griffiths' (1967, 1969) work on the development of feeding in young oystercatchers. Oystercatchers are specialist intertidal feeders of bivalve molluscs and other hard-shelled marine organisms. Norton-Griffiths found that they use either one of two different foraging techniques to open mussel shells. One technique is hammering through the shell of a tightly closed mussel and the second is stabbing between the gaping shells of a slightly opened mussel. Subsequent work by Goss-Custard *et al.* (1982) revealed that there are in fact two different hammering techniques: hammering of the dorsal or of the ventral surface of the mussel. Oystercatchers will tend to

specialize (though not exclusively) on one of these three methods (Goss-Custard & Sutherland, 1984). The young, however, are initially unable to exploit this food by themselves and, consequently, follow their parents to the feeding ground where they are supplied food until they are able to forage on their own. The age at which parental feeding ceases is variable -- it appears to depend on the time it takes the young to become self-sufficient. Young oystercatchers who feed on annelid worms can become proficient by 6 weeks of age, while young who feed on bivalves or crabs (which require a more difficult skill to open) take at least 12 weeks to become efficient. Norton-Griffiths (1968) determined through cross-fostering experiments that juvenile oystercatchers learn their technique from their parents.

Many other studies have only speculated that offspring are learning by watching their parents, but these claims have not been substantiated. For example, in killer whales, "intentional" beaching is a form of hunting used to capture elephant seals and sea lions (Lopez & Lopez, 1985). Juveniles have been seen to beach alongside an adult and it is believed the juveniles are learning the hunting technique from the adults. Dolphins have also been seen to beach themselves in pairs (believed to occasionally be an adult with a juvenile) in order to capture fish and that beaching is a behaviour juveniles learn from adults (Hoese, 1971). Cushing (1944) reviewed the literature on falconry and found that differences in specific food habits of various raptors are passed on from parent to offspring through "non-heritable" factors. In some cases, parents use specialized behaviours to favour local enhancement in their offspring. In red jungle fowl, the mother alerts her chicks when she finds food by giving food calls and exaggerated head movements and then dropping food in front of the chicks (Stokes, 1971). Diamond (1987) believes that juvenile tropical birds learn their foraging skills from their parents during the months spent together after fledging. Diamond's conclusions are based on the study by Werner and Sherry (1987), who observed juvenile Cocos finches following adults around and imitating their foraging techniques. Grant and Grant (1980) also believe that juvenile cactus finches acquiring new foraging skills by mimicking adults. All of these are field studies, and do not unequivocally demonstrate social learning from parent to offspring, but they do show, nevertheless, that opportunities for learning exist.

One of the few studies that brought parent-offspring social learning to the laboratory is Chesler's (1969). She compared the response of kittens observing their mother demonstrate a novel skill to obtain food with kittens who saw an unfamiliar female cat demonstrating the same skill. The skill involved lever-pressing to a visual stimulus. She found that the kittens who observed their mother demonstrate the task learned the response sooner than kittens who watched the strange cat. But this result may be partly due to the kittens' fear of an unknown cat, which may have affected its motivation to learn the skill. Kittens who had a strange cat as a demonstrator were less attentive the first day than those who had their mother as demonstrator. However, during the second day of trials, once the kittens were more familiar with the strange cat, there was no difference in attentiveness between the two groups.

In a laboratory study of social learning in rats, Galef (1977) found that learned feeding preferences of adult rats affected the feeding preferences of their young. When offered a choice of food their parents ate and food their parents had been trained to avoid, pups would choose the same diet as the parents. Although pups were attracted to particular feeding sites by the presence of their parents at these sites, pups who did not observe parents eating a particular food still chose their parents diet. This suggests that cues other than visual also play a role.

Flock Feeders versus Territorial Species

It is evident that little is actually known about social learning between parent and offspring, so that the question of parent-offspring transmission of foraging skills can still be explored. Chesler found that kittens learned faster when observing their mother. This result, as mentioned earlier, may 1 we been due partly to the an initial fear of the unfamiliar female cat. In solitary species, a juvenile's encounter with adults other than its parents may be rare and hostile, since parents usually chase off other adults. In such species, juveniles may learn from their parents because their parents are the only knowledgeable adults they can watch. If one finds juveniles copying the behaviours of their parents in such a situation, one cannot exclude possible genetic factors. One way to determine if juveniles are learning from their parents, while ruling out genetic factors, is to run experiments with cross-fostering, where juveniles are raised by adults other than their parents. Norton-Griffiths (1968) did this with oystercatchers. Another way to approach the problem is to look at learning in gregarious species.

In flock feeding species, juveniles feed with both parents and other nonrelated knowledgeable adults, so that juveniles become familiar with the other members of their flock. One can test if a juvenile will preferentially learn from parents by comparing learning between kin and non-kin demonstrators. Non-kin demonstrators would be other flock members that juveniles are familiar with. One way of testing this was seen in Chesler's work, which compared the learning rates of juveniles, half of which observed the mother demonstrating the task while the other half saw the strange female. A more direct approach is to have naive juveniles see both demonstrators and have the demonstrators perform different solutions to the same food-finding problem. The juvenile is then given the opportunity to perform both solutions in a choice-test situation. Whichever solution the juvenile initially performs should indicate which demonstrator it preferentially copies. The only study which has tested preferential social learning using this type of choice-test was that of Dolman (1991). She examined interspecific learning in the Zenaida dove by having naive Zenaida doves watch two demonstrators, one a conspecific, the other a grackle and found the naive dove copied the actions of the grackle; this preference makes biological sense, since the Zenaida dove is a territorial animal that is extremely aggressive towards conspecifics and often forages in mixed-species aggregations with grackles.

Thesis Goals

The goal of this thesis is thus to test for preferential learning from the parent in a flock feeding species. The study animal chosen was the ringdove, *Streptopelia risoria* - a domesticated descendent of the African collared dove, *Streptopelia roseogrisea* (Irwin, 1959, Goodwin, 1983). Wild collared doves are known to forage in small groups (Morel, 1983). Although ringdoves are, for the most part, a domesticated species, feral colonies have been established in Florida and in Los Angeles, California (Goodwin, 1983).

Ringdoves were chosen for this study because they have a long history as laboratory subjects and are easily bred and raised in controlled laboratory conditions. Many of the studies using ringdoves have looked at the effect of hormones on reproductive behaviour (e.g. Lehrman, 1955; Lehrman & Wortis, 1967 and Allen & Erickson, 1983), so a great deal is known about parent-offspring interactions in the species at least until juveniles reach independence. In particular, Wortis (1969) examined the behaviour of 14-day old squabs under various social conditions. At this age, juvenile ringdoves begin pecking at grain; Wortis examined what social factors affect this development by comparing pecking of squabs tested alone, with parents, with adults which had offspring of their own at different ages or adults without offspring. It was determined that the young had to be in a social situation in order to begin pecking at grain, since those that were placed in a test cage without adults within visual range failed to peck at the grain. When squabs were placed with foster parents, the frequency of their pecking was negatively correlated with the amount of regurgitation feeding received. Foster parents with older offspring regurgitated less and pecked more at grain themselves than foster parents with younger offspring. Regurgitation stimulated begging in the squabs while adults pecking at grain seemed to prevent begging and stimulate pecking in the test squabs. Graf et al. (1985) also looked at the development of pecking in the ringdove by comparing the amount of pecking shown by juveniles aged 13 to 22 days and raised in four different conditions: their parents were given either seed or powdered grain, and the interval was either negligible or extended between the test and the juveniles' return to their purents home cage. Graf et al. found that if ringdoves were raised on powdered food, normal levels of pecking failed to develop when the exposure to seed was not in close temporal proximity to interactions with parents. Thus, parent-juvenile interactions have been shown to be important in the development of pecking in young ringdoves. It would therefore seem logical to conclude that parents may also play an important role in other areas of foraging and that the opportunities are there for social learning to occur since juveniles begin foraging alongside their parents. This is what the present thesis explores.

This study is divided into four experiments. The first experiment looks at the social behaviour of juvenile ringdoves bred and raised in our laboratory for the purposes of this study. Laboratory breeding allows complete control of juvenile associations with kin and non-kin before the experimental phase of the study. The ringdoves are then observed in an aviary setting to determine whom they forage with and how they interact with adults, both related (their parents) and non-related flock members. Little is known about how juveniles ringdoves interact in such flock situations. The last three chapters describe choice-tests given to juvenile ringdoves, in which three important components of foraging behaviour are considered: learning of environmental colour cues associated with the presence of food, learning of new food types, and learning of a novel food searching technique. In these choice-tests, the juvenile observed two demonstrators (one related, one non-related), each providing different information about the novel foraging situation. One demonstrator was always the juvenile's father. The father was selected as the related demonstrator because it is usually the parent who feeds post-fledging columbids (Hitchcock & Mirarchi, 1984). Juvenile doves are known to be able to recognize their fathers; Hitchcock et al. (1989) used playback experiments to show that both nestlings and fledgling mourning doves respond more to their father's perch-coo with food-soliciting behaviour than to a neighbouring male's perch-coo.

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جر ۲ The second demonstrator was a familiar but unrelated flock member (either male or female) which had been foraging in the aviary with the juvenile in the week prior to the choice-test experiments. Given that both related and unrelated demonstrators provide conflicting information about the novel foraging situation, we expect the juvenile to match the choice made by the father in a two-choice test if the juvenile selectively uses the information provided by kin.

CHAPTER 1 - AVIARY STUDY

INTRODUCTION

In order for social learning of foraging skills to occur, it is important that juveniles actively forage with other individuals; it is from this association that opportunities arise for a naive individual to learn about foraging by seeing other flock members forage. Usually, other flock members are conspecifies, but in the case of territorial birds, flock members can be birds of other species. In such a case, individuals can potentially learn by watching individuals of other species. In field studies, Dolman (1991) found that Zenaida doves most frequently foraged either alone or in the company of Carib grackles; grackles thus offered the greatest potential social source of foraging information to the Zenaida doves. In laboratory choice-tests, the Zenaida doves preferentially copied the grackle's solution over another Zenaida dove's solution (Dolman, 1991). This shows that foraging associations play an important part in determining who individuals will learn from.

Choice-tests of the type conducted by Dolman have not been done on homospecific flocks. In such flocks, the most obvious factor to test is relatedness, by comparing kin and non-kin flock members as sources of social learning. The review of post-fledging parental care presented in the general introduction suggests that the potential for social learning to occur in parent-offspring associations is clearly present. In gregarious birds, few studies have examined whether post-fledging juveniles preferentially associate with kin. One such study was done by Stamps *et al.* (1990), who examined the social interactions of fledgling budgerigars in an aviary. They found that newly independent budgerigars tended to initiate more social interactions than expected with their siblings and their father.

Data of this type are not available for ringdoves. The goal of this chapter is thus to determine how newly independent juvenile ringdoves interact in small aviary flocks composed of kin and non-kin members. If preference for learning from kin is to be tested, one must first confirm that kin are a potential source of information; i.e. that juvenile ringdoves preferentially forage with kin.

METHODS

Subjects

All thirty-two juveniles used in this experiment were bred in our laboratory. Pairs of adults were placed in breeding cages (38 x 60 x 38 cm.) which contained a perch and a nest bowl (14.5 cm. in diameter) filled with pigeon grit. Pairs of doves were visually isolated from other pairs. Food (a commercial mixture of seed) and water was provided ad libitum. Each pair of doves would incubate one or two eggs until they hatched (at fourteen days). Once doves hatched, any subsequent eggs laid by the mother during the test period were removed. The young doves were raised by their parents and remained in the breeding cage until they were 4 weeks of age. At this point, the kin group was removed from the breeding cage and placed in an aviary (1.5 x 2.5 x 3.0 m.); approximately one hour later, a pair of adult doves, unrelated to the kin group, were placed into the same aviary. Two identical aviaries were available so that experiments could be run concurrently on two separate flocks. In each aviary, approximately 60 g, of seed mix/day was scattered into the sawdust covering the aviary floor. Birds had to search for food, a situation that was designed to mimic foraging situations in the wild. The experiments were conducted between August and December of 1987.

Procedure

The kin group and the two unrelated flock members remained together in the aviary for about one week. During this time, 4 two-hour sessions of the ringdoves foraging were videotaped. The video camera was placed outside the aviary during the taping and was focused on approximately half of the floor of the aviary. Sessions were always taped immediately after 60 g. of seed was scattered into the sawdust, on the half of the floor which was in view of the camera. The taping sessions were randomly distributed throughout the day, between 10 a.m. and 7 p.m. Only one session per aviary was videotaped on any given day. The individual flock members were identified by either distinctive feather colouration or by added markings to the wings and / or tail feathers.

The videotapes were analysed by scan sampling the sessions at 30 second intervals. At each scan, the identity of the doves and the activity of the juvenile(s),

whenever observed: begging, regurgitation, aggression and local enhancement. Food begging occurs when a juvenile extends its upper torso toward another individual, while flapping its wings and making upward lunges of its bill towards the other individual's bill. This is coupled with vocalizations by the juvenile, commonly called 'squeals' (Wortis, 1969). Regurgitation is when an adult feeds a juvenile crop-milk by vigourous pumping movements of its upper torso. Aggression occurs when an individual is chased by, pecked at or wing-slapped by another individual. Local enhancement is defined as occuring when a juvenile approaches a feeding individual and starts feeding close to it (i.e. within one body length).

Only the first hour of each session was analysed. However, if juveniles did not forage during this hour, the second hour was then analyzed. This was the case in 8 of the 128 sessions videotaped.

RESULTS

Initially, data from all four sessions for each juvenile were kept separate. However, there were not enough data collected from continuous sampling of the four behavioural variables for statistical analysis to be possible on a session-by-session basis, and, consequently, the data from all 4 sessions were pooled. Twenty (10 male, 10 female) of the thirty-two juveniles were raised with a sibling, while the remaining twelve (6 male, 6 female) juveniles were from single-offspring clutches. The sex of the juveniles was determined after all the experiments had been conducted, i.e. once the juveniles reached maturity. Gender was determined from observing courtship and reproductive behaviours since male and female ringdoves are externally isomorphic.

Data for juvenile association were collected from the scan samples. An association frequency was defined as the number of scans a juvenile was seen foraging with another member of the flock. Association frequencies were assessed by a twoway (juvenile sex x flock member) analysis of variance, with repeated measures over the second factor. Since juveniles with a sibling associated with one more flock member (its sibling) than single juveniles, data for these two groups of juveniles were analysed separately; the design is thus a 2×5 ANOVA for juveniles with a sibling and a 2×4 ANOVA for those without siblings (Table 1). Within the ANOVA's, planned comparisons were done to test three effects: (1) a juvenile's association with its sibling versus its association with the adults in the flock, (2) a juvenile's association with its parents versus its association with the unrelated flock members and (3) juvenile gender on its association with the other flock members. Juveniles with siblings associated more often with their siblings than with the adult flock members (F(1,72) = 58.42, P < 0.01). Juveniles from both groups associated more often with their parents than with the unrelated flock members (with sibling: F(1,72) = 52.18, P < 0.01; without sibling: F(1,30) = 9.33, P < 0.01). There was no significant difference in association between juvenile females and juveniles males.

All instances of local enhancement directed towards each of the other flock members (collected from continuous sampling) were summed for every juvenile. These frequencies were also analysed by a two-way analysis of variance with repeated measures for the flock members. Once again, juveniles with a sibling were analysed separately from juveniles without a sibling (Table 2). As with the association data, three planned comparisons were done to test: (1) a juvenile's frequency of approach to its foraging sibling versus its frequency of approach to the foraging adults in the flock, (2) a juvenile's approach to its parents versus its approach to the unrelated flock members and (3) the effect of juvenile gender on its joining of other flock members. For juveniles with siblings, juveniles joined their foraging sibling more often than they joined the adults of the flock (F(1,72) = 28.03, P < 0.01). Juveniles of both groups joined their foraging parents more often than they joined unrelated flock members (with sibling: F(1,72) = 6.65, P < 0.05; without sibling: F(1,30) = 12.12, P < 0.01). There was no significant gender effect with respect to the frequencies of local enhancement.

These differences in local enhancement could reflect preferential joining of specific types of flock members or they could simply be spurious effects of the unequal association frequencies revealed above; a juvenile could thus approach its foraging sibling more often because both are foraging on the ground more often. In order to determine this, the local enhancement data were then compared to the proportion of observed foraging associations of each flock member with the focal juveniles. Individual frequencies in each group were summed and the totals of foraging associations (Table 3) and local enhancement (Table 4) compared via a goodness-of-fit test. The distribution of local enhancement frequencies was not

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significantly different from the distribution of foraging association (see X^2 values in Table 4).

In all the sessions, there were very few instances of begging observed. Five juveniles begged from their father, four from their mother, and two juveniles begged from both the unrelated male and female flock member None of the juveniles begged from their sibling. Forty-two of the fifty-two begging incidents observed came from one pair of male siblings. Because of its infrequent occurence, no further analysis was carried out on the begging data. Regurgitation was also rare; the father was observed regurgitating to a begging juvenile on only nine occasions.

Aggression between adults was observed but not analysed. Occasionally, adult ringdoves were aggressive towards the juveniles and vice versa, but juveniles were not aggressive towards each other. Since there was no sibling aggression, data from all juvenile males were combined as were data from all juvenile females. Aggression was analysed by a two-way analysis of variance with repeated measures, but because of the low frequencies of aggression, mother and father aggression was combined, as were aggression from the unrelated male and the unrelated female; this effectively compares aggression coming from adult kin and adult non-kin (Table 5). There was no juvenile sex effect, but there was a significant difference between kin and non-kin (F(1,30) = 11.52, P = 0.002); non-kin were more aggressive towards the juveniles. There was also an interaction effect, where the kin were more aggressive towards male offspring.

As in the case of local enhancement, the frequency distribution of aggressive acts directed toward the juveniles was compared to the association frequency with the adults (from Table 3). In all cases, the distribution was significantly different (Table 6). The majority of cases of aggression were from the unrelated flock members, while the mothers virtually never attacked their offspring.

DISCUSSION

The data on foraging associations revealed that, when there was a sibling, juvenile ringdoves foraged most often with that sibling. Juveniles also foraged more frequently with their parents than with unrelated flock members. These results are consistent with other studies which have shown that juvenile birds frequently associate with other juveniles and with kin members (Stamps *et. al.* 1990; Hötker, 1982).

Although the absolute frequencies of local enhancement were directed more towards kin, the juveniles' joining frequencies were related to frequency of foraging association. Aggression, on the other hand, was seen most often between juveniles and non-kin. Overall, these results suggest that juvenile ringdoves forage more with kin than non-kin, possibily because foraging with kin is less disrupted by aggression. Parents may be more tolerant because they have a genetic interest in their own offspring.

The results indicate that when there is a sibling, juvenile ringdoves are on the ground foraging most often with that sibling. Juveniles may simply be associating with their sibling more often because the adults are involved in other activities, i.e. courting, and/or mate defense, and, as a result, the adults are not as often on the ground. In addition, physiological constraints can be keeping both juveniles on the ground longer and therefore together. Firstly, juvenile birds are often inefficient foragers and therefore must forage for longer periods of time than adults. This has been observed in a variety of species including royal terns (Buckley & Buckley, 1974), herring gulls (MacLean, 1986) and northern mockingbirds (Breitwisch, *et al.*, 1987). Inefficient foraging may also be the case here. Secondly, immature flight structures may also be keeping the juveniles on the ground more often, in that their flying ability may be poorly developed (Marchetti & Price, 1989).

In terms of social learning of foraging information, although siblings are the most frequent associates of juvenile ringdoves, the siblings are no more knowledgeable in foraging skills than the juveniles themselves; therefore siblings cannot be expected to be major social contributors of foraging information, even though they are most frequent associates. Conceivably, potential sources of information should be from knowledgeable individuals, i.e. the adults. If we compare the absolute frequencies of foraging association and local enhancement between juvenile ringdoves with the adults, we find juveniles forage more often with their parents than with non-kin. There

is also less aggression between parents and juveniles than between non-kin and juveniles. These results indicate that the potential for learning from the parents is greater than from non-kin.

However, if scrounging occurs, foraging associations and local enhancement may not necessarily lead to learning. Giraldeau and Lefebvre (1987) found that if individuals share in the food discoveries of others, this often inhibits learning of the food-finding technique. However, Lefebvre (1986) showed that there are situations where learning is not blocked by scrounging. In the subsequent choice-tests of this study, juveniles are unable to share in the food discoveries of the demonstrators and this should therefore not inhibit their learning of the foraging skills.

CHAPTER 2 - VISUAL CUES IN THE ENVIRONMENT

INTRODUCTION

In order to find food, one foraging skill which juveniles must learn is to associate food with certain features in the environment. This can be done by observing where others feed and by linking environmental cues found at feeding sites with food. Environmental cues can include such things as specific locations, specific shapes, or colours associated with food. In laboratory studies, colours are often used as visual cues to food location. For example, Edwards *et al.* (1980) have shown that pigeons can learn to discriminate red and green colour keys by observing a trained demonstrator pigeon peck at a red key to obtain food. Mason *et al.* (1984) paired food with yellow or green food cups to test observational learning of preferences and aversions in red-winged blackbirds. Goforth and Baskett (1971) had mourning doves feed freely on food located against four different coloured substrates and found the mourning doves preferred specific colours. Food consumption was greatest against a blue background, next was red which was preferred over green, and the lowest consumption was against yellow.

This experiment examines social learning of a colour cue by juvenile ringdoves. For this experiment, the two adult demonstrators (father and unrelated flock member) were trained to associate a particular colour with food by learning to remove either a red or green coloured lid which covered a well containing seed. The juvenile ringdove would see one demonstrator finding food under a red lid and the other demonstrator finding food under a green lid. The juvenile was then presented with two covered food-wells; one was covered with a red lid, the other with a green lid. If the juvenile selectively used the information provided by its father, it should then, upon presentation of both coloured lids, select the colour which its father chose.

METHODS

Subjects and Apparatus

The ringdoves used in this experiment were the same thirty-two juveniles used in the previous experiment. Juveniles were tested between the ages of 35-53 days. The experiments were conducted between August and December of 1987. For approximately one week before testing, a juvenile remained in a freeflight aviary along with its sibling (if there was one), its parents, and two unrelated adult ringdoves. During that week, the videotaping sessions of the previous chapter were done. Food was always available *ad libitum* until it was removed from the aviary the evening prior to testing. The juveniles were tested in the afternoon at an average of 92% of their *ad libitum* weight. One hour prior to testing, a juvenile, its father and one of the flock members were removed from the aviary and placed in individual testing cages (28 x 38 x 29 cm.). There were two openings (4 x 5 cm each) at the front of each cage from where the ringdove could extend its head out to feed from the apparatus placed outside the cage. The juvenile's cage was placed so that it faced the front of both demonstrators' cages at a distance of 30 cm. (Fig. 1).

The apparatus used in the experiment was a black wooden tray $(10 \times 22 \text{ cm.})$ on which two food-wells (2.5 cm. in diameter, 1 cm. deep) were attached (14 cm. apart, so that a food-well was available at each opening of the cage). Each food-well had a circular metal lid (3 cm. in diameter) whose upper portion was lined with coloured cardboard. One food-well was covered by a green lid while the other was covered by a red lid (Fig. 2). These colours were chosen since mourning doves had intermediate preferences for them. Demonstrators were presented this tray with food (an average of 20 millet seeds) located under only one of the two coloured lids. One demonstrator had food available under the green lid, while the other demonstrator had food available under the green lid, while the other demonstrator had food available under the red lid. However, when the juvenile was subsequently presented with the tray, food was available under both colours (20 millet seeds /food-well).

Procedure

Prior to testing each juvenile, the two adult demonstrators were pre-trained to remove either a red or green coloured lid off a food-well in order to obtain seed. The colour choice was counterbalanced between the father and the unrelated flock member. The training was accomplished through shaping, where the food-wells were progressively covered with the coloured lid on successive trials as the dove ate from the well. The sex of the flock member to be used in the experiment was counterbalanced, so that half the juveniles had an unrelated male flock demonstrator, while the other half had an unrelated female flock demonstrator. Immediately before testing, each juvenile was presented with a tray on which there was only one uncovered food-well. The juveniles were allowed to eat a few seeds from the apparatus. This food-well was successively presented on both sides to avoid a positional bias. Food was provided to prime the juvenile. The order of the position of the food-wells presented to the juveniles was randomized across individuals tested.

Each trial was videotaped. During a trial, the juvenile was given 5 demonstrations of lid removal alternately by each demonstrator. For the 10 demonstrations, the position of the appropriate colour and the order of presentation of the demonstrators (i.e. father then flock member or flock member then father) were randomized. The demonstrators were then removed and the juvenile was presented with the tray containing food under both the red and green lids. The juvenile was allowed up to 15 minutes to uncover one of the lids and eat from the food-well underneath. The initial choice made by the juvenile was recorded along with the latency to choosing. Prior to analysis, the latencies were subsequently transformed to their natural log in order to normalize their distribution. If the juvenile did not make a choice within 15 minutes, the demonstrators were returned and the juvenile was given 10 more demonstrations. The demonstrators were once again removed and the juvenile was given 15 more minutes to remove a lid and eat. This procedure was repeated up to two times, if necessary, for a total of 30 demonstrations, thereby giving the juvenile a total of 45 minutes to make a choice. If the juvenile failed to do so after this time, the experiment was stopped, and the juvenile was considered not to have learned the task. Juveniles were returned to ad libitum feeding after a random delay of between 5 minutes to one hour after testing.

RESULTS

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Twenty-nine of the thirty-two juveniles tested opened one of the two foodwells, but there was no preferential copying of either demonstrator. Fifteen juveniles selected the colour their father chose, while fourteen selected the colour the flock member chose ($X^2 = 0.03$, df = 1, p > 0.90, Fig. 3). If instead, we compare the colour choice made by the juveniles, 18 chose the red lid, while 11 chose the green (Fig. 4), so the initial choice of lids made by the juveniles was not significantly biased towards a particular colour ($X^2 = 1.69$, df = 1, p > 0.10). Nor was the choice based on a positional preference, since 13 juveniles chose the lid on the left side of the tray while 16 chose the lid on the right side ($X^2 = 0.31$, df = 1, p > 0.50).

If we compare the choices made based on the latencies to opening of a foodwell, there was no difference in latencies between those who matched the colour of their father's food lid or those who matched the colour of the flock member's food lid (t-statistic = -0.52, dt = 27, two-tailed p = 0.61). Nor was there any difference in latencies between those juveniles choosing red and those choosing green lids (tstatistic = -1.43, df = 27, two-tailed p = 0.16).

There were no significant interaction effects between task and demonstrator or between demonstrator and subjects: colour vs. demonstrator (Fisher test, p = 0.18), demonstrator vs. sex of the flock member (p = 0.56), demonstrator vs. sex of the juvenile (p = 0.43), nor demonstrator vs. age of the juvenile (Mann Whitney U test; U = 83, p > 0.05). Other interactions were also tested (e.g. colour vs. sex of flock member) but none were significant.

DISCUSSION

The results of this experiment indicate that juvenile ringdoves showed no preference to match the colour choice of either demonstrator. The juveniles appeared to randomly choose a colour, although there was a slight, but non-significant preference for red. This trend is in the same direction as the colour preferences observed in mourning doves, where Goforth and Baskett (1971) also found that red was slightly preferred over green.

In a design of the type used here, a negative result can always be interpreted as a failure by the animals to attune to the cues the experimenter has chosen to vary. For instance, lack of demonstrator preference could simply mean that doves are copying the lid-removal behaviour of the demonstrators and disregarding both colour and demonstration identity. One way to eliminate this possibility is to use a much more complicated design, as Palameta (1989) has done to examine social learning of colour cues in canaries, using successful versus unsuccessful demonstrators and knowledgeable versus naive observers. In this type of experiment, food is associated with one type of environmental cue (for instance, red lids) and observers are either given (knowledgeable) or not given (naive) the opportunity to watch a successful demonstrator finding food with the help of this cue and an unsuccessful demonstrator failing to find food when interacting with other cues (e.g. green lids). If social learning occurs, knowledgeable observers are then expected to show discrimination between the correct and the incorrect cue upon their first encounter with the foodfinding problem, i.e. before their own trial-and-error learning can start operating. Palameta found that knowledgeable canaries could learn the appropriate colour cue associated with food by watching conspecifics.

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A design of this type is difficult to apply to the problem studied in this thesis, however, since the kin versus non-kin demonstrator effect has to be added to the other variables in Palameta's design. This increases the number of groups, and thus the sample sizes required, to a magnitude that is difficult to manage with laboratory-bred and raised subjects, which necessitate much more time and care than wild-caught or commercially bought animals.

The design of comparing equally efficient solutions to the task is thus the only design that could realistically test for demonstrator preference in the present case. Where demonstrator preferences exist, this design is perfectly capable of bringing them out. Dolman (1991) has used the same design as the one used in this thesis to examine conspecific versus heterospecific demonstrator preferences in Zenaida doves. In one of her experiments, naive Zenaida doves watched two demonstrators (a conspecific and a grackle) eat novel foods associated with different colour rues; the novel food was cooked rice dyed red (for one of the demonstrators) or green (for the other demonstrator). Thus, in Dolman's experiment, the only difference between the two demonstrators' solutions was the colour of the rice. Dolman's results showed that even with equally efficient solutions, naive Zenaida doves preferred to copy the heterospecific's choice of food. The negative results of the present experiment can thus be interpreted as a genuine lack of demonstrator preference and not as a spurious result of the design.

CHAPTER 3 - NOVEL SEED CHOICE

INTRODUCTION

One important problem that juveniles must solve when foraging is recognizing what in the environment is consumable as food. Food recognition may be pre-programmed (e.g. loggerhead shrikes and American kestrels appear to have an inborn recognition of mice; Smith, 1973; Mueller, 1974) or learned by individual trialand-error, or it can be learned by observing the food choices of knowledgeable individuals. In some species, offspring are known to copy the food choices of their parents. For example, although the pecking response in precocial birds may be innate, chicks must still learn to distinguish food from non-food. In red junglefowl, specialized behaviours by the mother hen allow her to attract her chicks to food she has located (Stokes, 1971). Subsequently, the chicks will peck at the same objects that the hen pecked at or held in front of them. In the laboratory, Turner (1964) had chicks observe a mechanical model of a hen peck at green-coloured grain. He found that in a choice-test of green and orange coloured grain, the chicks subsequently pecked more often at the green grain. Further studies by Suboski & Bartashunas (1984) confirmed these results that young chicks were selectively pecking at the grain they saw a hen model peck at; such factors as innate colour or position preferences, reinforcement effects and social facilitation were ruled out as possible explanations for this copying.

In zebra finches, Rabinowitch (1969) examined the way in which early experiences with particular seed types affected later seed preferences. He found that juveniles would preferentially select seeds they had been raised on. If juveniles were raised on one seed type throughout the nestling period and a second seed type during the fledgling period, they preferred the seed type they encountered during the fledging period. Since it is during this time that juveniles follow their parents around, it may be that juveniles acquire preferences for the seed type they are exposed to during this association. Similar results were obtained in ringdoves (Csermely, 1980), where it was found that a juvenile's early experience with certain seeds can influence their seed preference later on.

This experiment examines the learning of new food types in the juvenile ringdove. Juveniles are presented with two novel seed types: one seed type it sees its father eat, the other seed type it sees the unrelated flock member eat. The experiment is designed to determine if juvenile ringdoves will copy their fathers' choice of seed.

METHODS

Subjects and Apparatus

The twenty-two juveniles used for this experiment were bred in the laboratory from August 1988 to March 1989 in the same manner as the juveniles that were used in the two previous experiments. When the juveniles were three weeks old, they were transferred, along with their parents and two unrelated adult flock members, from a breeding cage to an aviary. In the aviary, seed was provided *ad libitum*, but for the first few days was hidden in the sawdust covering the floor so that the juveniles could gain some experience searching for food. During testing days, however, the seed was provided in a bowl to facilitate its removal on the evening prior to each test. Both in the breeding cage and in the aviary, the doves were fed a commercial mixture of seeds that did not contain either of the novel seed types to be used in the experiment.

Juveniles were tested between the ages of 24 and 40 days. Approximately one hour prior to testing, the juvenile and the two adult demonstrators were placed in individual test cages 17 cm apart, facing each other (as in the previous experiment). Wooden blocks ($21 \times 8 \times 10.5 \text{ cm}$) covered in green velvet were placed in front of each cage. Green velvet was used as a substrate for two reasons: 1) it provided a contrasting background for both seeds and, 2) the plush of the velvet kept the seeds from scattering.

Testing Procedure

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The novel seeds used were flax (*Linum usitatissimum*) and canary seed (*Phalaris canariensis*), which are approximately the same shape and size, but differed in colour. Two days prior to the experiment, both adult demonstrators were removed from the aviary for short periods of time to allow them to eat the new seed types to be used in the experiment. This provided them the opportunity to eat the new seed types in the absence of the juveniles.

The experiment consisted of eight 3-minute trials per juvenile. For every trial, each demonstrator was presented with 0.5 g. of one of the two types of seed, while the juvenile was presented with 0.5 g. of each new seed type. The initial seed type of each demonstrator was randomized. The juvenile and the two demonstrators were

simultaneously presented with seed, so that the juvenile could eat at the same time as the demonstrators. The juveniles were allowed to sample both seed types during a trial. Trials were ended earlier than 3 minutes if the juvenile completely depleted one of the seed types, since a depletion eliminated the possibility of making a choice. For trials 1 to 4, the seed type of each demonstrator remained the same. At trial five, the seed type given to each demonstrator was reversed to counterbalance demonstrator with seed type.

All sessions were videotaped. For each trial, the first choice made by the juvenile was recorded, along with the latency to eating. The latencies were transformed to their natural log in order to normalize their distribution. Seeds were weighed at the start and at the end of each trial. The amount eaten during a trial could thus be obtained by subtraction and transformed into number of seeds consumed by calibrating a seed number per unit weight ratio for each seed type. For flax, this ratio was $103 (\pm 10)$ seeds/g., while for canary seed, it was $91 (\pm 10)$ seeds/g.

RESULTS

The choice of first seed eaten by the juveniles is the best measure of social learning since this choice is not influenced by any subsequent individual assessment by the juvenile on the value of the seed as food. In choosing which seed type to eat first, the juveniles tested showed no preference for either their father's or the unrelated flock member's type of seed. Twelve juveniles initially chose the seed type that their father was eating, while ten juveniles initially chose the seed type of the unrelated flock member (Fig. 5) ($X^2 = 0.18$, df = 1, p > 0.70). This lack of demonstrator preference was consistent over all eight trials when the number of trials of each choice per individual is compared (paired t = 1.53, df = 21, two-tailed p = 0.14).

However, contrary to the results of the preceding chapter (where juveniles showed no colour preference), there was a clear initial preference in this experiment for a particular seed type regardless of the demonstrator that was eating it. Seventeen juveniles first chose the flax seed, while only five chose the canary seed ($X^2 = 6.55$, df = 1, p < 0.02), (Fig. 6). Due to sampling of the other seed type in subsequent trials, however, this initial preference for flax does not remain sufficiently stable to reach

statistical significance throughout the eight trials (paired t = 1.77, df = 21, two-tailed p = 0.09).

Another measure of preference for a particular demonstrator is the total consumption of the seed type eaten by a particular demonstrator. Total comsumption can be measured either in weight (grams) or in number of seeds eaten. In both cases, the result is the same - there is no overall preference for a particular demonstrator (weight: Wilcoxon signed rank test, T = 72, N = 21, p > 0.05; number: T = 71, N = 22, p > 0.05). Only one of the twenty-two juveniles ate only the seed type consumed by its father. All others ate some amount of both seed types. When comparing the total consumption of each seed type over all trials, the majority of juveniles continued to show a preference for flax (weight: Wilcoxon signed rank test, T = 46.5, N = 21, p < 0.02; number: T = 39, N = 22, p < 0.01). Only three of the twenty-two juveniles tested ate more of the canary seed than flax.

There was no left-right position effect ($X^2 = 0.73$, df = 1, 0.30 > p > 0.50), nor any interaction effect between the demonstrator and the seed type (Fisher test, p = 0.59).

In comparing the latencies to eating of the first seed, there is no difference between those juveniles initially choosing the father's seed type versus those choosing the unrelated flock member's seed type (t = -0.97, df = 20, two-tailed p = 0.35). There is also no difference between the latencies of those choosing flax first versus those choosing canary seed first (t = 0.90, df = 20, two-tailed p = 0.38).

To determine the effect of trials on latency, the data from all juveniles were combined, since there was no significant difference in latency between individuals regardless of the choice made. A comparison of latencies to first seed eaten across the eight trials rev. aled a significant effect of trials (one way ANOVA, repeated measures, F(7,21) = 11.12, p < 0.001). This effect is mainly due to the decrease in latency from trial one to trial two. A trend analysis of average latency per trial across all trials yields a good fit to a logarithmic function (y = $3.19x^0.31$), with an r² of 0.86 (Fig. 7). This function gives a better fit than a negative linear function (r² = 0.71).

DISCUSSION

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In this experiment, the seed type the juvenile ringdoves first chose to eat did not reveal a preference for seed eaten by a particular demonstrator. This lack of preference was reflected both in terms of the initial seed type chosen and the latency to eating of the first seed. Even throughout the eight trials, when first choice per trial was measured, no demonstrator preference was evident. However, there was a preference for a particular seed type, since flax was more often the initial choice of seed. The amount of flax consumed per juvenile over the eight trials was also significantly greater than the amount of canary seed consumed. There was, however, no difference in latencies between initial choice of seed type, nor was the first choice of seed type per trial consistent over all trials.

Although there was an overall preference for flax seed, it was not eaten exclusively, nor was it the preferred seed of all individuals. This indicates that there was sampling of both seed types and that there was individual variation with respect to seed preference. Individual differences in seed preferences has been previously demonstrated in captive pigeons feeding singly by Moon and Zeigler (1979) and in feral pigeons feeding in groups by Giraldeau and Lefebvre (1985). Thus it appears that the results found in pigeons also hold true for other gregarious Columbids. Variation in seed preference among individuals can lead to intraspecific resource partitioning. This is a way for gregarious foragers to reduce intraspecific competition through modification of diet choice. Inman, Lefebvre and Giraldeau (1987) have shown evidence that this can occur in pigeons, while Lefebvre and Robidoux (1991) suggest that dominance may play an important role in regulating this system.

CHAPTER 4 - NOVEL MOTOR TASK

INTRODUCTION

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Not only must a juvenile learn where to find food and how to recognize it, but specific skills may also be required to search for and handle food that is not immediately visible in the environment. For example, young oystercatchers must learn the technique of opening mussel shells before they can exploit this food (Norton-Griffiths, 1967). Juvenile herring gulls are also required to learn specific digging skills when foraging through rubbish in a garbage dump (Verbeek, 1977).

Several laboratory studies have examined the acquisition of foraging skills by presenting birds with novel situations in which to search for food. In greenfinches, chaffinches and canaries, Vince (1958) compared the learning of string-pulling to obtain food between juveniles and adults. Dawson and Foss (1965) tested social learning of different lid removal techniques in budgerigars. Sasvári (1985) tested several species of tits and thrushes on three different techniques for revealing hidden food: 1) pulling a string out of a test tube in order to obtain food attached to end of the string, 2) picking up a vertical piece of cloth to uncover food in hole beneath and, 3) pulling out a drawer containing food within. Palameta (1989) had demonstrator pigeons use several different obstacle removal techniques, including sliding or piercing a disk, removing a stopper, or rotating a wheel in order to expose hidden food. Although obstacle removal may be learned by trial and error, Palameta (1989) showed that pigeons can learn a specific motor act by imitation of conspecifics performing the task.

This experiment examines the learning of a novel food-searching technique. As in the previous experiments of this thesis, the juvenile sees two demonstrators (its father and an unrelated flock member) performing two novel tasks. The apparatus used is designed so that there are two separate obstacles concealing food. Each of the demonstrators is trained to solve one of the two tasks by manipulating different locations on the same apparatus. After observing the demonstration of both tasks, the juvenile is presented with the apparatus and can reveal the hidden food by solving either of the two tasks. Thus the task that the juvenile solves gives an indication of which demonstrator it learned from.

METHODS

Subjects and Apparatus

The twenty-two juveniles used in this experiment were all previously tested in the seed choice experiment. The seed choice experiment provides no specific experience that is likely to bias the present experiment in one direction or another. After being tested in the seed choice experiment, the juveniles were returned to the aviary and remained there for 2 to 9 days before being tested on the motor task experiment.

The apparatus used in the experiment was a box $(5.5 \times 5.7 \times 5.0 \text{ cm})$ constructed of transparent plexiglas and covered in order to render it opaque. The box had a circular food-well recessed into the top, fitted with a 2.5 cm lid. A drawer was built into the box, half way up the front (Fig. 8). A metal loop was attached to both the lid and drawer, enabling a dove to either lift the lid off or pull the drawer open in order to reveal concealed food.

The placement of the test cages in this experiment was different from the two previous experiments. Here, the juvenile's cage was placed so that the juvenile did face the demonstrators directly, but, instead, had a side view of them. To insure that the juvenile was able to view both demonstrations equally well, its cage was moved 30 cm sideways between positions A and B (Fig. 9) depending on the demonstration.

Procedure

Demonstrators were trained to perform only one of the two tasks. The assignment of tasks to the demonstrators was counterbalanced over all juveniles tested. The training of the demonstrators again involved shaping. Initially they were allowed to eat from an open drawer or a non-obstructed food-well on the top of the box. On successive shaping trials, either the drawer was progressively closed or the lid was placed closer to the food-well, until it completely fit into it. If the dove showed no response to a completely closed apparatus, seed was attached to the appropriate loop to direct the dove's pecking at that loop. If this still failed to produce the right response, they would be given demonstrations of the task by another dove who had already learned the task.

Food was removed from the aviary at approximately 6 p.m. of the night prior to testing. All trials took place the following afternoon. Approximately one hour prior to testing, the two adult demonstrators were removed from the aviary and placed in individual cages (as in the previous experiments). They were presented with the testing apparatus in order to re-familiarize them with the task they were to perform. The juvenile was then placed in its individual testing cage. Fifteen to thirty minutes prior to testing, the juvenile was permitted to watch each demonstrator eat from the open apparatus, i.e. there was no lid covering the top food-well and the loop was removed from the opened drawer. The juvenile was then presented with the apparatus and allowed to eat 20 millet seeds from each open location on successive presentations of the apparatus. The order of presentation of seed at the two locations was counterbalanced across all juveniles tested.

The testing phase of the experiment involved ten trials. Each trial consisted of the juvenile watching one demonstration of each task, followed by a three minute period, where it was presented with the closed apparatus containing seed in both sections. The order of task presentation was counterbalanced throughout. If the juvenile managed to open one of the sections and eat the seed, the apparatus would be removed before the end of the three minutes. If the juvenile succeeded in opening one of the sections on three consecutive trials, this section of the apparatus was sealed on the following trials to determine if the juvenile could learn the other task. If the other section was also successfully opened on three consecutive trials, the sealed section was unsealed for the remaining trials. All trials were videotaped and the following variables were recorded: (1) location and latency of the first peck on the apparatus, (2) location and latency of the first section to be displaced - even if not necessarily opened, and (3) location and latency of the first seed eaten. Also, the number of pecks directed at each section (top and drawer) was counted. All latencies were transformed to their natural log in order to normalize their distribution.

In order to control for individual learning and to make sure that the techniques used were learned by observation, the juveniles were divided into two groups. One group received demonstrations of both tasks, while the second (control) group was tested without receiving any demonstrations from the adults, although they were allowed to eat from the open apparatus. Individuals from the control group who failed to learn the task on their own were re-tested 3 to 9 days later with demonstrations in order to determine if they were capable of learning the task socially.

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RESULTS

Assessment of learning of the novel food searching technique was divided into three actions performed by the juveniles: (1) initial contact of the juvenile's beak on the appropriate location on the apparatus, (2) actual displacement (or movement) of a section of the apparatus caused by a pull or a nudge from the beak of the juvenile, (as a tug at a loop may be enough to partially open one of the sections without exposing food or at least provide some feedback about the apparatus), and (3) actual opening of one of the sections of the apparatus by the juvenile, where hidden food is thereby exposed and eaten. This last action is the best measure of imitation (and the most difficult response). In each case, the location for each action can indicate which demonstrator was copied. All 11 of the juveniles in the experimental group made contact with the apparatus, while 10 succeeded in displacing at least one of the sections and of these, 9 actually were able to open a section and eat.

Five out of eleven juveniles first pecked at the same location of the apparatus their father interacted with, while six first pecked at the location the unrelated flock member interacted with (Fig. 10). This would indicate no preference for either demonstrator in terms of location of first peck made ($X^2 = 0.09$, df = 1, p > 0.90). In terms of section first displaced, four juveniles first displaced the section of the apparatus demonstrated by their father, while six juveniles first displaced the section demonstrated by the unrelated flock member, and one juvenile failed to displace either section (Fig. 11). There was again no preference to attempt the task demonstrated by either adult ($X^2 = 0.40$, df = 1, p > 0.50). Seven juveniles were successful at opening and eating from the section demonstrated by the unrelated flock member, while only two juveniles were successful at opening and eating from the section demonstrated by their father (n = 9, Sign test, p = 0.18, two-tailed, Fig. 12).

When the total number of pecks made to each section of the apparatus prior to obstacle removal is compared, there is no preference to peck at either the section demonstrated by the father or the section demonstrated by the unrelated flock member (Wilcoxon signed-rank, N = 9, z = -0.357, two-tailed p = 0.72).

There was no difference in latency to first peck, latency to first displacement or latency to eating between those juveniles who chose the task demonstrated by their father and those who chose the task demonstrated by the unrelated flock member (Mann-Whitney U test, U = 15, $n_1 = 5$, $n_2 = 6$, p = 0.54, U = 18, $n_1 = 4$, $n_2 = 6$, p = 0.13, U = 3, $n_1 = 2$, $n_2 = 7$, p = 0.17 respectively).

If the location of the first peck is compared, ten juveniles directed their first peck at the front drawer section and one juvenile first pecked at the top lid section (Fig. 13). The location of the first peck at the apparatus thus appeared to be influenced by the apparatus itself ($X^2 = 7.36$, df = 1, p < 0.01). Although not significant, it was the top lid of the apparatus that was more often initially displaced -- eight juveniles first displaced the top lid and two juveniles first displaced the front drawer ($X^2 = 3.60$, df = 1, p < 0.10),(Fig. 14). Again the top lid was more often successfully opened, but not significantly so -- with seven juveniles eating from the top first and two eating from the front drawer first (n = 9, Sign test, p = 0.18, two-tailed, Fig. 15). However, the location of the first peck was not correlated with the first section that was actually displaced by the juvenile (Sign test, p = 0.17, one-tail), nor was it correlated with the section the juvenile first ate from (Sign test, p = 0.25, one-tail).

There is also no difference in latency to first peck, latency to first displacement or latency to eating, in those juveniles who chose the front drawer versus those who chose the top lid (Mann-Whitney U test, U = 6, $n_1 = 1$, $n_2 = 10$, p = 0.36, U = 6, $n_1 = 2$, $n_2 = 8$, p = 0.36, U = 1, $n_1 = 2$, $n_2 = 7$, p = 0.06 respectively).

There is no overall preference to peck at a particular section if we compare the total number of pecks made to each section (Wilcoxon signed-rank, N = 9, z = -1.01, two-tailed p = 0.31) regardless of the demonstrators' choices. There were no interactions between demonstrator and task for either first peck made (Fisher test, p = 0.54), first displacement (Fisher test, p = 0.67), or first section to eat from (Fisher test, p = 0.58).

There was no significant difference between the experimental and control groups in terms of number of juveniles pecking at the apparatus. All eleven juveniles who received demonstrations pecked at the apparatus, while ten out of eleven juveniles receiving no demonstrations still pecked at the apparatus ($X^2 = 1.05$, df = 1, p = 0.31). There is, however, a significant difference between the groups with respect to the number of juveniles successfully opening one of the sections and eating the seed within. In the group receiving demonstrations, nine out of eleven were successful at opening at least one of the sections and eating while in the control group only three juveniles out of eleven did so ($X^2 = 6.60$, df = 1, p = 0.01). This indicates that

although most juveniles will peck at the apparatus, those who saw demonstrations of the tasks were able to learn to solve the task in much higher numbers. In both the experimental group and the control group, the section of the apparatus which was preferrentially pecked at first was the front (drawer) (experimental: $X^2 = 7.36$, df = 1, p < 0.01; control: $X^2 = 3.60$, df = 1, p < 0.05).

Demonstrations of both tasks were repeated over ten trials not only to determine the juveniles first choice, but also to determine if the juveniles were able to repeat the task they performed. Of the nine juveniles who were able to successfully open and eat from one of the sections, five actually went on to repeat the task in three consecutive trials. Three of these juveniles opened the top section on three consecutive trials, while the other two repeatedly opened the front section. Of the three juveniles in the control group who received no demonstrations but still managed to successfully open at least one section, none in fact performed the task three times.

If juveniles were able to repeat a task on three occasions, it was assumed that they had successfully mastered that task. On subsequent trials, therefore, this part of the apparatus was made unopenable, in order to determine if the juveniles were capable of performing the other task. Only one of the five juveniles who had one section sealed went on the learn the second task. Another juvenile did manage to open and eat from both sections, but did not repeat either task three times.

Juveniles in the control group were re-tested with demonstrations at a later date to determine if, upon demonstration of the task, they would be able to learn it. Of the eleven, four juveniles did open and eat from one of the sections (this included two who previously opened a section without demonstrations) and all four were able to repeat the task three consecutive times. Two of the juveniles also managed to open and eat from the other section.

We can compare the choices made by the juveniles in both the novel seed experiment and the motor task experiment, since the same juveniles were tested in both. Of the nine juveniles who succeeded in learning the motor task, four of them matched the choice of the same demonstrator in both experiments, while five juveniles matched the choice of one demonstrator in one experiment and the choice of the other demonstrator in the other experiment. There is therefore no consistency within individuals in terms of learning from a particular demonstrator.

DISCUSSION

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As in the previous experiments, there was no preference for the juvenile to match the choice of either demonstrator. No matter what variable was tested, the results were consistent. Instead of showing a preference for a particular demonstrator, the juveniles showed a preference for a particular section of the apparatus. An initial preference to peck at the front drawer may have been due to the fact that the front loop is the closest part of the apparatus to the juvenile. Even though the drawer was the first part of the apparatus to be pecked at, it was usually not the first task solved. It would appear that the lifting of the lid off the top of the apparatus was perhaps the easier of the two tasks to perform and thus more juveniles learned it first. It is difficult to design an apparatus consisting of two different tasks and make them equally easy to solve. However, in this case, the location and degree of difficulty of the tasks were balanced so that even though the drawer was pecked at first, it was the more difficult of the two tasks to perform.

GENERAL DISCUSSION

The Kin Preference Hypothesis

Taken together, the results of the choice-test experiments in the last three chapters of this thesis clearly point to a lack of preference for the father as a social demonstrator of foraging behaviour in juvenile ringdoves. When juveniles observed both their father and an unrelated flock member provide equally appropriate solutions to a foraging problem and obtain equal reward, the father was never preferentially copied. This held true for environmental cues associated with food, for novel seed type and for novel food searching behaviours. The results of these choice-tests are summarized in Table 7. All demonstrator related variables showed non-significant effects with alpha probability levels up to 0.90, with more than half of them greater than 0.50. These values indicate a random choice with respect to demonstrator. Thus the only conclusion that can be made is that there was no preference for either demonstrator.

In_tead, the choice made by the juveniles appeared to be influenced more by the apparatus itself than by the demonstrator identity. Of the twenty-six key variables examined in the three experiments, only three showed a significant preference and these preferences were all related to the task itself: juveniles preferred flax seed in chapter three and tended to initially peck at the front drawer of the apparatus in chapter four. Of the task-related variables that were non-significant, all but two were below the 0.20 alpha probability level. These low probability levels suggest there may have been other borderline effects that could conceivably reach traditional significance levels with either increased sample sizes or changes in procedure which may bring out possible effects blurred by the techniques used here. However, these potential preferences are taskrelated biases and thus would not change the overall conclusions of this study. Other possible preference effects not included in Table 7 were all controlled by counterbalancing procedures in the experimental design. These include left-right positioning, order of presentation, sex of the unrelated flock members, and any interactions of these variables with demonstrator identity and task. As expected, all these effects were nonsignificant.

Since both demonstrators showed equally relevant solutions to a foraging problem and both demonstrators obtained equal amounts of food for their efforts, one

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may argue that this design cannot show preference since the rewards are equal. The only other way to test for demonstrator preference is to have one demonstrator provide an appropriate solution and the other demonstrator provide an inappropriate solution. This was the design used by Dolman (1991). In this type of design, however, one may potentially mask significant preferences if there are confounding effects of taskrelevance with demonstrator type and if demonstrator preference is weak. In such cases, large sample sizes would be required to clarify any interaction or weak preference effects. This is not a problem if one uses easily caught wild birds as Dolman did, but the more time-consuming and labour-intensive procedure of laboratory breeding used in the present thesis placed more severe limitations on sample size. In addition, if there was a demonstrator preference, as was the case in Dolman (1991), this demonstrator preference would logically be more easily revealed in the type of design used in this study, where no irrelevant solution existed to potentially work against a demonstrator preference.

Thus, the experiments described in this thesis represent a stringent test of the parent-preference hypothesis. Firstly, multiple experiments were conducted to test the hypothesis under several aspects of foraging, and in all situations, the same negative conclusions can be drawn. Secondly, a gregarious species was chosen to compare parents with other familiar, knowledgeable adults that juveniles forage with in order to specifically test for parent preference. One has a much weaker test of the hypothesis if one tests a species where juveniles only encounter their parents foraging, since juveniles are not likely to receive alternative sources of information from unrelated individuals. In these cases, no alternative pathway exists for the transmission of foraging skills.

However, this lack of parent-preference does not imply that in field conditions juveniles of gregarious species will not learn more often from their parents than from other adults. Chapter one of this thesis showed that in ringdoves, juveniles foraged more often with their parents and were aggressed more by non-kin. Because of these two factors, social learning from the parent could occur more often simply due to probability factors in the same way that local enhancement was seen to occur most often with kin. If social learning is a simple function of frequency of association, juveniles may learn more from their kin simply because they have more opportunities to observe kin than non-kin.

<u>Mechanisms</u>

In social learning, the separation of various sources of information needed to pin-point mechanisms of transmission requires detailed experiments such as the ones performed by Palameta & Lefebvre (1985) and Palameta (1989). This was not the goal of the present study and the numerous control groups needed to determine the precise mechanisms were consequently not done here. Therefore, in this study, one cannot claim that learning was accomplished through precise novel motor act imitation of a demonstrator (see Lefebvre & Palameta (1988) and Palameta (1989) for a discussion of terminology and criteria needed in determining exact mechanisms). In fact, juveniles probably acquire new skills in several different ways and in many different contexts; therefore a range of mechanisms are probably used by them, depending on what is to be learned. For example, social facilitation may be sufficient in learning a new food type, but imitation may be required if a new motor skill is to be mastered. The central question of this thesis addressed who juveniles learned from, and not how they learned.

One may argue, however, that a possible explanation for the non-significant demonstrator preference is that in fact the juveniles did not watch or learn from the demonstrators and subsequently made all their choices individually. However, the motor task experiment provides evidence that this possibility can be effectively ruled out. Although the motor task experiment was the only one where the precise role of social versus non-social sources of information was examined, it nonetheless found that social cues were necessary for the high performance levels seen in the group of juveniles who received demonstrations. Only 3 of the eleven birds tested without a demonstration solved one of the tasks, while nine of 11 birds given a demonstration succeeded in opening one of the two sections of the food box. Although controls of this type were not done in the colour cues or the novel seed type experiments, one can reasonably speculate that social cues were also attended to in these experiments. Other more anecdotal sources of evidence also point to the attendance of social cues. In all the experiments, food-deprived juveniles were attracted to the feeding demonstrators and clearly observed them when they manipulated the food-producing apparatus. Juveniles would orient themselves towards the demonstrator side of their cage and often extend their heads out of the opening in the front of their cage that was closest to the performing demonstrator. In addition, several of the demonstrators used in the motor task experiment were unable to learn the task simply through shaping procedures. These individuals did, however, learn the task after they saw other demonstrators perform it. If we consider these behavioural arguments along with those that stem from the low performance of the control birds in the motor task experiment, we can reject the idea that no demonstrator preference indicates nonattendance to the demonstrators.

In the motor task experiment, control and experimental birds did not differ in latency to pecking at the apparatus, but for the control birds, the latency to first displacement and first opening was significantly greater than for the juveniles who received demonstrations. This would seem to indicate that the initial contact with the apparatus does not depend on social cues. However, if we consider the significant difference in the number of juvenile ringdoves actually learning a task between the experimental and control groups, and the low proportion of birds from the control group who learned even once demonstrations were given, we find that the main effect of demonstrators seems to be in influencing persistence at manipulating the apparatus and perhaps providing specific technical information about opening movements to the observers.

Other non-social forms of learning mechanisms can also be ruled out. Spontaneous performance can be eliminated as a possible mechanism since very few birds that were not provided with demonstrations actually succeeded in revealing the food. Shaping can also be discounted since prior exposure to an open apparatus was not sufficient in enabling the juveniles of the control group to open a closed box. In chickadees, Sherry and Galef (1984) had shown that this kind of prior experience with cream-tubs was sufficient to explain later opening in a large percentage of birds; this was not the case here.

In choice-test experiments of colour cues and novel seed type, the mechanisms involved are more difficult to pin-point, since the features incorporated into the motor-task experiment were not applicable to the other two studies. In order to isolate the effects of environmental cues and novel food type, one has to minimize effects related to the motor task itself. In the novel seed experiment, no motor task was required to reveal hidden food since the food was openly available. The important aspect to be learned by the juveniles was if the new seed types were edible (i.e. if it was not poisonous or of no nutritional value). The safest way for juveniles to determine this would be through stimulus enhancement, where the juveniles see the knowledgeable demonstrators eating the seed type and subsequently copy the

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demonstrators' choice of food. However, since juveniles were able to eat concurrently with the demonstrators, one cannot rule out social facilitation in this case.

In the colour cues experiment, the motor act of removing the lid was not required to be novel and subsequently learned socially, since it was the colour choice of the lid that was important. Lid removal, nonetheless, could have been learned socially either by imitation of either of the demonstrators or more simply through stimulus enhancement, where the juveniles' attention was drawn to the lids, by seeing demonstrators remove the lids and eat from the uncovered food-wells. The juveniles could not have learned the lid-removal task through social facilitation, because the demonstrators were not visible to them when they were presented with the covered food-wells. Indirect evidence from chapter four suggests that prior exposure to an open dish, which was provided in both these experiments (colour cues and motor task), was not sufficient to lead to high frequencies of opening in birds not given a social demonstration. However, in the absence of controls specific to the task presented in the colour cues experiment, any definitive conclusions about the mechanisms involved in solving this task must be deferred.

Parent-Offspring Transmission of Song Learning

We can compare learning of foraging skills with that of song learning in zebra finches, where parent-offspring transmission has been examined in a number of studies in order to determine if young male zebra finches learns their father's song. While Böhner (1990) claims that they do, Williams (1990) found that juvenile male zebra finches do not preferentially copy their father's song. It appears that the conditions the zebra finches were raised in affects who they learn from. Böhner's zebra finches were raised in individual cages while Williams' zebra finches were raised in an aviary. Slater and Richards (1990) found that juvenile male zebra finches were more likely to incorporate song elements from their father if the father was unable to re-nest. It seems that the fathers that re-nested spent less time interacting with their offspring and thus the father's songs were less likely to be copied by their offspring. In a field study of wild zebra finches in Australia, Zahn (1990) confirmed that the majority of young male finches do learn their song phrases from their father. In addition, Zahn found that the younger the juveniles were captured and isolated from their fathers, the lower were the matching scores with their fathers. These findings in song learning seem to parallel the findings of this study, where the juveniles appear to be opportunistic learners, in that they probably learn from the knowledgeable individuals that they spend the most time with, since they get most information from these individuals. Thus, in the field, because juveniles spend a great deal of time with their parents, they inevitably appear to learn from them.

Implications of this Study

The present results may have implications for mathematical and evolutionary models of cultural transmission, since many of these models assume that vertical, i.e. parent-offspring, transmission is a key route for the spread of both novel and traditional behaviours. The present experiments suggest that parent-offspring transmission may often not differ from other channels of social learning within a group. This result has important ramifications for co-evolutionary theories of gene-culture interactions. When cultural transmission is restricted to or highly biased in favour of kin, as may be the case in parent-offspring transmission of behaviours in territorial species, there is inevitably a high degree of overlap between genetic and cultural pathways. Offspring can show the same behaviours as their parents whether the mechanism of transmission is genetic or cultural. In addition, juveniles may not have access to the potentially greater, non-kin related pool of behavioural information present in the population at large.

In contrast, when juveniles learn from unrelated individuals as easily or more easily than from kin, cultural and genetic pathways interact in a different way. Innovations that appear within a given kin unit can spread to individuals outside that unit. Any genetic advantage initially associated with the innovation eventually disappears, since broad cultural access to the behaviour renders differential reproduction with respect to this trait unimportant. An additional complicating factor is the question of compatibility between the genetic and cultural components of a given behaviour. If a parent transmits to its offspring both the genetic and cultural components for a given behaviour, one can safely assume that these components are compatible since they function adequately in the parental demonstrator. When the demonstrator is unrelated, however, parental genotypes and non-parental "culturtypes" do not necessarily fit together.

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The complexity of this question can be illustrated by the tit milk-drinking example given by Wyles, *et al.* (1983), who suggest that anatomical evolution can potentially be driven by behavioural change. If the new behaviour of bottle-opening spreads in a tit population, this may provide the selective context for alleles favouring the enzymatic breakdown of milk proteins, normally of low frequency in birds, to also spread. If bottle opening is transmitted from parent to offspring, so too would be the lactose-digesting enzymes needed to digest the milk. This would lead to the rapid development of a phenotypic linkage between the bottle-opening traditions and the appropriate alleles needed to drink the milk within the bottles. When cultural transmission occurs between non-kin, this kind of co-evolution would undoubtedly be much slower, especially so if there is interspecific transmission; this effectively has occurred in the bottle-opening example, as up to eleven passerine species have exhibited the behaviour (Hinde and Fisher, 1951).

The precise, quantitative impact of kin versus non-kin transmission has yet to be incorporated in specific mathematical models of cultural transmission. In fact, such models usually to not take into account the empirical findings available in the animal literature and they are based on *a priori* theoretical assumptions. It is inevitable that the frequently paradoxical results obtained from experimental work on animals will sooner or later have to be incorporated into these models if they are to become more realistic and useful. Factors such as the frequency-dependent inhibition of social learning caused by scrounging (Giraldeau & Lefebvre, 1987), the preference for heterospecific demonstrators in territorial species (Dolman, 1991) and the lack of kin-biased transmission in a group forager (this thesis) will significantly complicate but also enrich the study of cultural learning at the population level.

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Repeated measures analysis of variance on frequencies of association. Juveniles with siblings analysed separately from juveniles without a sibling.

Source of variation	df	MS	F	Р
(Juveniles with sibling)				
Between subjects effects				
Sex Error	1 18	1128.960 7799.227	0.145	0.708
Within subject effects				
Flock member Flock member x Sex Error	4 4 72	227 13.710 471.410 810.082	28.076 0.582	0.000 0.677
(Juveniles without siblings)				
Between subjects effects				
Sex Error	1 10	363.000 5308.192	0.068	0.799
Within subject effects				
Flock member Flock member x Sex Error	3 3 30	3069.694 840.722 961.253	3.193 0.875	0.038 0.465

Repeated measures analysis of variance on local enhancement. Juveniles with siblings analysed separately from juveniles without a sibling.

Source of variation	df	MS	F	Р
(Juveniles with sibling)				
Between subjects effect [*]				
Sex Error	1 18	0.250 15.726	0.016	0.901
Within subject effects				
Flock member Flock member x Sex Error	4 4 72	31.615 1.075 3.639	8.687 0.295	0.000 0.880
(Juveniles without siblings	3)			
Between subjects effects				
Sex Error	1 10	0.083 28.183	0.003	0.958
Within subject effects				
Flock member Flock member x Sex Error	3 3 30	32.250 7.694 6.606	4.882 1.165	0.007 0.339

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Frequencies of foraging associations. The total number of scans juveniles from each category are seen foraging with each of the other flock members.

		** 7* . 1.			
Juvenile	Sibling	With Father	With Mother	With Unrelated Male	With Unrelated Female
Females with sibling	1320	1080	1092	617	460
Males with sibling	1307	883	952	574	508
Females with- out sibling		505	443	270	229
Males with- out sibling		324	437	285	269

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Frequencies of local enhancement, the total number of times juveniles from each category approached each foraging flock member. Chi square values compare these frequencies to expected values based on the proportion of foraging frequencies (from Table 3) of each flock member. All chi-squares are non-significant (df = 4, juveniles with sibling; df = 3, juveniles without sibling).

Juvenile	To Sibling	To Father	To Mother	To Unrelated Male	To Unrelated Female	X ²
Females with sibling	46	32	28	20	18	3.0
Males with sibling	51	25	30	17	16	2.3
Females with- out sibling		30	35	10	9	7.5
Males with- out sibling		17	32	16	17	2.0

Repeated measures analysis of variance on frequencies of aggression of kin versus nonkin. Sibling not considered a category since there was no aggression observed between siblings.

Source of variation	df	MS	F	Р	
Between subjects effects	\$				
Sex Error	1 30	20.250 12.658	1.600	0.216	
Within subject effects					
Relatedness Relatedness x Sex Error	1 4 30	182.250 90.250 15.817	11.523 5.706	0.002 0.023	

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Frequencies of aggression, the number of times attacks or chases were directed to juveniles in each category. X^2 is the result of comparing these frequencies to expected values based on the proportion of foraging frequencies (from Table 2) of each adult flock member (df = 4, juveniles with sibling; df = 3, juveniles without a sibling; p < 0.001 in all cases).

Juvenile	From Fath er	From Mother	From Unrelated Male	From Unrelated Female	X ²
Females with sibling	3	1	17	6	40.9
Males with sibling	0	0	16	16	61.9
Females with- out sibling	17	0	9	5	13.8
Males with- out sibling	1	0	54	7	150.4

Summary of choice test results. Comparison of preference effects for all variables tested in all three choice-test experiments. N.S. indicates no significant preference found. Significance levels in parenthesis. Significant effects are in bold type.

Variable tested:	Environmental Cues Expt.		Novel Seed Type Expt.		Novel Motor Task Expt.	
	Demon- stratror	Colour	Demon- strator	Seed Type	Demon- strator	Motor Task
1st peck made	N.S. (>0.90)	N.S. (>0.10)	N.S. (>0.70)	FLAX (<0.02)	N.S. (>0.90)	FRONT (<0.01)
latency of first choice	N.S. (0.61)	N.S. (0.16)	N.S. (0.35)	N.S. (0.38)	N.S. (0.54)	N.S. (0.36)
total 1st choices			N.S (0.14)	N.S. (0.09)		_
# seeds consumed			N.S. (>0.05)	FLAX (<0.02)	_	
# pecks to apparatus	_				N.S. (0.72)	N.S. (0.18)
1st displace- ment	_			_	N.S. (>0.50)	N.S. (>0.05)
latency of displacement	-			—	N.S. (0.13)	N.S. (0.36)
1st to eat	_	_			N.S. (0.18)	N.S. (0.18)
latency to eating	_			-	N.S. (0.17)	N.S. (0.06)

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Figure 2

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DEMONSTRATOR IDENTITY





LID COLOUR CHOSEN



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DEMONSTRATOR IDENTITY

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SEED TYPE

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TRIALS



Figure 8

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Figure 9








DEMONSTRATOR IDENTITY

Figure 11



SECTION OF APPARATUS

Figure 12

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A. 4.....

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SECTION OF APPARATUS

Figure 14

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DEMONSTRATOR IDENTITY

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Figure 15



SECTION OF APPARATUS