Mode of Foraging Competition Is Related to Tutor Preference in *Zenaida aurita*

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This study compared the direction of social learning in 2 populations of Barbados Zenaida doves *(Zenaida aurita)*. One population (St. James) is territorial; it competes aggressively with conspecifics but scramble competes with heterospecifics. The other population (Deep Water Harbour) forages in large homospecific flocks. Field observations were conducted to quantify intraspecific and interspecific patterns of foraging association and aggression. Wild-caught doves from both areas were then tested on novel foraging tasks demonstrated by either a conspecific or a heterospecific tutor. In all experiments, St. James doves learned more readily from the heterospecific tutor (Carib grackle *[Quiscalus lugubris]*), whereas Deep Water Harbour doves learned more readily from the conspecific tutor. The type of competitive feeding interaction in the field (i.e., scramble vs. interference) appears to better predict the pattern of social learning in an experiment than does species identity.

Studies of interspecific variation in learning have often used the comparative method (Balda & Kamil, 1990; Domjan & Galef, 1983; Kamil, 1988; Krebs, Healy, & Shettleworth, 1990) to test the idea that differences in learning specializations are adaptive and therefore correlated with differences in foraging ecology (Rozin & Kalat, 1971; Sherry & Schacter, 1987; Shettleworth, 1993). More than 35 years ago, Klopfer (1959, 1961) anticipated these modern trends when he proposed two hypotheses to account for interspecific variation in social learning: (a) Solitary species should exhibit less social learning than gregarious ones, and (b) conservative species should exhibit fewer or different forms of social learning abilities than opportunistic ones. Several studies have since stressed the link between group living and social learning on the one hand (Altmann, 1989; Emlen & Oring, 1977; Krebs, MacRoberts, & Cullen, 1972; Strupp & Levitsky, 1984) and between opportunism and social learning on the other (Gandolfi, 1975; Sasvari, 1979, 1985; Strupp & Levitsky, 1984).

Recent work on Columbids and other species, however, has questioned the quantitative link between ecology and social learning. In comparing group-living feral pigeons *(Columba livia)* and territorial Zenaida doves *(Zenaida aurita)*, Lefebvre, Palameta, and Hatch (in press) found that pigeons consistently outperformed *Z. aurita* on all learning tests, whether social or nonsocial. In reanalyzing similar comparative work done by Klopfer (1959) and Sasvari (1979, 1985) on six passerine species, Lefebvre and Giraldeau (in press) concluded that there was little evidence for adaptive specialization in social learning related either to group living or opportunism: In all species tested, consistent interspecific differences in both social and individual learning appeared to mask any specialized, quantitative effects of foraging ecology.

In this article, we attempt to circumvent these problems by linking intraspecific differences in feeding competition with qualitative effects on the direction of social learning. Following Palameta (1989), we used feeding competition, not social organization, as a predictor of social learning, comparing the effects of scramble and interference competition. In scramble competition, animals attempt to remove food as quickly as possible from the reach of others by ingesting or hoarding it; in interference competition, animals attempt to remove others from the vicinity of food by defending it. Speed is therefore the key to success in scramble competition, as opposed to aggression in interference competition. Because social learning allows an observer to rapidly reduce the temporary feeding advantage held by a knowledgeable individual, scramble competition may represent an important selective context for this form of learning, leading to a form of "mental arms race" (Palameta, 1989).

We focus on two Zenaida dove populations in Barbados whose mode of feeding competition appears to be radically different. One population, that of coastal St. James (StJ), is territorial: Zenaida doves there forage most often alone but frequently associate with heterospecifics in nonaggressive mixed-species aggregations (Lefebvre et al., in press);

mated pairs appear to defend their feeding and nesting area against conspecifics year-round. The other population, that of the Deep Water Harbour (DWH), forages in large homospecific flocks (personal observation) in much the same way as feral pigeons do in temperate ports (Lévesque & McNeil, 1986; Murton, Coombs, & Thearle, 1972): in this population, interactions with heterospecifics appear to be infrequent, and feeding competition with conspecifics seems to be predominantly regulated by scramble competition rather than aggression. Both populations, like all Z. aurita in Barbados, are highly opportunistic and urbanized (Haverschmidt, 1969), occupying the same niche as C. livia (Lack, 1976; Pinchon, 1963) and the collared dove (Streptopelia decaocto; Hutt, 1979) do in other countries. In the first part of this article, we present quantitative field data on demography, aggression rates, and foraging group size of Z. aurita and its avian feeding associates in coastal StJ and at DWH. In the second part, we use the contrasting modes of feeding competition in the two populations to test the association between ecology and learning. More specifically, we ask whether population differences in competition against conspecifics and heterospecifics influence the type of tutor species most likely to favor social learning. We tested Zenaida doves captured in coastal StJ and at DWH on social learning tasks rewarded with food, offering them the choice between a conspecific and a heterospecific tutor.

If social learning pathways are flexible and covary with the types of foraging interactions experienced by an animal in the field, we predict that Zenaida doves from DWH, which scramble compete for resources with conspecifics, should learn more readily from the conspecific than the heterospecific tutor. Conversely, we predict that doves from coastal StJ, which use scramble competition with birds of other species but interference competition against conspecifics, should show the reverse tutor preference, learning more readily from heterospecifics. Such a finding of ecologically correlated learning differences within a single species would question the assumption (e.g., Sherry & Schacter, 1987; Shettleworth, 1993) that learning specializations are necessarily the result of divergent natural selection. Alternatively, if social learning pathways are species typical and linked to interspecific genetic differences, then group-living Zenaida doves from DWH should show the same tutor preference as territorial doves from coastal StJ.

Field Study

Method

Field observations were conducted in two main areas of Barbados, the parish of StJ and DWH. Preliminary observations suggested that these areas featured two very different forms of Zenaida dove social organization. In StJ, doves defend year-round territories and forage most often alone (Lefebvre et al., in press). In contrast, at DWH, Zenaida doves appear to forage in large, nonaggressive flocks (personal observations). The StJ area sampled consists of a 6.48-km coastal stretch that includes beaches, hotel and restaurant grounds, public parks, and private residences;

for observational purposes, the width of the coastal stretch varies between 10 and 50 m. The area features extensive coastal woodland, consisting mainly of manchineel, mahogany, casuarina, and coconut trees, which offer ideal roosting and nesting sites for Zenaida doves (Bond, 1985). DWH consists of a landfilled area, approximately 150×200 m^2, that includes docking, grain loading, milling, and storage facilities. The zone has been cleared of most of its arboreal vegetation but provides large, ephemeral patches of spilled grain (wheat and maize) and legumes (soybean) as a result of transport or storage operations.

Three sets of data were collected in the two areas: (a) foraging group size distributions of Zenaida doves, (b) number of individuals per site for Zenaida doves and the five avian species they forage with; and (c) rates of intraspecific and interspecific aggression involving Zenaida doves. For group size distributions, walking censuses were taken on different days in December–January and April–May, between 7:00 and 10:00 a.m. These months correspond, respectively, to the beginning and the end of the dry season, according to local rainfall records, and represent the two yearly extremes in food and water availability (Caribbean Meteorological Institute, 1982). The number of Zenaida doves seen feeding or searching for food on the ground was noted, as well as the size of the foraging group to which these birds belonged. Doves were considered to be part of the same foraging group if they were separated by less than 5 m, the criterion used in a previous study comparing Zenaida doves and feral pigeons (Lefebvre et al., in press).

The mean number of birds per site was recorded for the six avian species that forage in polyspecific aggregations in Barbados: Zenaida doves (Z. aurita), Carib grackles (Quiscalus lugubris), glossy cowbirds (Molothurus bonariensis), common ground doves (Columbina passerina), Lesser Antillean bullfinches (Loxigilla noctis), and feral pigeons (C. livia). In StJ, data were recorded by two observers. One observer recorded all foraging associations every 30 s, and the other scanned the site continuously, noting intra- and interspecific aggression. A foraging association included any birds foraging within one body length of each other. Foraging was defined as a bird feeding or searching for food with frequent pecks at the ground. An aggressive act was defined as a peck, wing slap, or chase involving a Zenaida dove. Threat displays (ritualized beak swipes at the ground or raising of the wing contralateral to the opponent) were not included because they could bias the data through their almost exclusive use in intraspecific encounters.

To better mimic the conditions that apply at DWH, where large amounts of food are periodically made available to the birds through spillage, we conducted observations in StJ both with and without provisioning. For the unprovisioned data, four replicate sessions, each lasting 50 min, were conducted at five different sites (a total of 1,000 min of observations). The five sites (a public park, a residential area, and the grounds of three different hotels, each corresponding to the approximate surface of the DWH area sampled) were separated by an average of 250 m and were all strongly affected by human activity. Provisioned observations were conducted at the same five sites. Provisioned trials were conducted before unprovisioned ones: a minimum of 5 days separated the two types of trials at a given site to avoid any carryover effects of provisioning. For each provisioned trial, nine patches of cooked white rice (5 g each), spread over 50 cm^2, were distributed in a 3×3 array, with 2 m separating each patch. This 16-m^2 area fits within the territory of a single pair of Zenaida doves (the mean ground diameter of a territory is approximately 20 m, as defined by area defended by ritualized threats). Trials were therefore conducted at four different locations within the five field sites to cover the territories of different doves. A provisioned trial began when a

bird started foraging in one of the patches and ended (on average, after 9.34 min) when the rice had been completely eaten or when all birds had ceased to feed for at least 10 min. Between 5:30 and 8:00 a.m.. five replicate trials were conducted on different days at each of the four locations of the five sites, yielding 100 trials (a total of 934 min, approximately equivalent to the unprovisioned data set). The field study in StJ was conducted during the middle of the dry season.

At DWH, a single observer recorded foraging associations every 3 min for 9 hr (in 1-hr sessions over 3 days) between 8:00 a.m. and 2:00 p.m.. yielding 180 counts. Acts of aggression involving Zenaida doves were tabulated by scanning the site every 30 s for 10 hr over 3 days at the start of the dry season. The number of Zenaida doves foraging was also recorded during this session, so that aggression frequencies could be transformed to rates per individual. An average scan of the site took 20 s of the 30-s interscan interval.

From these three sets of data (StJ unprovisioned, StJ provisioned, and DWH), a random sample of 100 scans was taken, and the probability of a Zenaida dove feeding alone, with conspecifics, with grackles, or with both conspecifics and grackles was calculated. Grackles were chosen for this variable because they were the only major foraging associate of Zenaida doves present in both areas.

Results and Discussion

Two hundred eighteen and 216 Zenaida doves were seen in the walking censuses conducted at the start and end of the dry season, respectively. Figure 1 illustrates the proportion of birds in each area seen foraging alone or in groups of 2. 3. or 4 or more individuals. In StJ. the median group size was 1 for both sampling periods, with almost all birds foraging alone or in pairs. At DWH. the median group size was 32 for the start. and 9 for the end. of the dry season. The probabilities of foraging alone were .07 and .09 in the two seasons at DWH. These values are much closer to the .02 probability of foraging alone recorded for feral pigeons in Montreal (Lefebvre et al., in press) than they are to the .69–.71 found for Zenaida doves in StJ (Table 1). Comparisons of group size distributions within each area and between areas for a given season revealed no seasonal differences within areas but significant differences between areas (Table 1). In all of these comparisons, data were lumped into two categories. foraging alone or foraging with others, because of small sample sizes in many of the categories illustrated in Figure 1.

Table 2 presents the mean number of birds per count for each of the six avian species, as well as the frequency and rate of intra- and interspecific aggression. Zenaida doves from StJ were much more aggressive and much less numerous in relation to other avian species than they were at DWH. During provisioned trials, an average of 1.2 doves attended the rice patches, with a total of 1,374 aggressive acts, or a rate of 76.3 acts per dove per hour. Carib grackles were attracted in relatively large numbers by the provisioned patches (7.9 grackles per count), but interspecific aggression between doves and grackles was low (17 acts). During unprovisioned trials, a mean of 3.6 Zenaida doves were seen at the sites in StJ (a site comprises several territories), with an intraspecific aggression rate (468 acts,
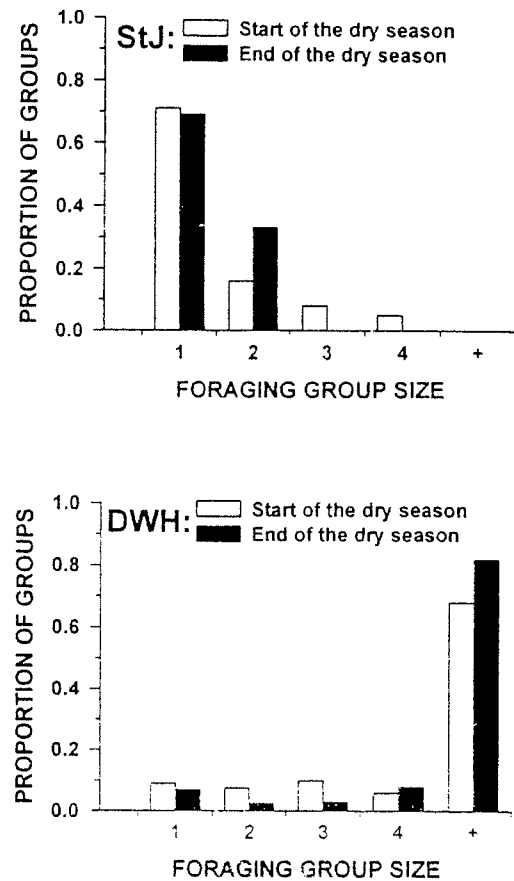

Figure 1. Proportion of Zenaida doves observed foraging alone or in groups of 2. 3. or 4 or more at the start and end of the dry season in St. James (StJ; top panel) and at the Deep Water Harbour (DWH; bottom panel).

or a rate of 7.7 acts per dove per hour) that was intermediate between the one recorded for DWH and the provisioned trials in StJ. Interspecific aggression was as low in unprovisioned trials (10 acts) as it was in provisioned ones, with mean grackle numbers lower than they were when rice patches were provided (2.6). It should be noted that our definition of aggression actually underestimates the difference between intra- and interspecific interference competition: If we had included threat displays, which are almost exclusively directed to other doves, we would have obtained an even larger effect. Aside from *Q. lugubris*, the mean number of birds for the other species was low in both studies of StJ. and no interspecific aggression was observed between these species and *Z. aurita*.

DWH was characterized by large numbers of Zenaida doves and low numbers of individuals from the five other species. No acts of interspecific aggression were seen. Intraspecific aggression was relatively infrequent: 267 acts were seen in 10 hr for a mean of 33.9 doves. a rate of 0.79 acts per dove per hour (doves were less numerous in this estimate than in the one given in Table 2 because the area scanned in these sessions was slightly smaller). When the

Table 1

Median Group Size, Probability of Foraging Alone, and Sample Size at the Start and End of the Dry Season

Season	St. James	Deep Water Harbour	$\chi^2(1)$	p
Start of dry season			86.40	<.001
Median group size	1	32		
Probability of foraging alone	.69	.07		
Sample size	110	108		
End of dry season			85.00	<.001
Median group size	1	9		
Probability of foraging alone	.71	.09		
Sample size	83	133		
$\chi^2(1)$	0.02	0.05		
p	ns	ns		

Note. Chi-square values refer to differences between distributions within sites (vertical) and between adjacent sites (horizontal).

20-s mean duration of scans per 30 s was translated to continuous time to allow comparison with the observations in StJ, the hourly rate reached 1.18 acts per dove per hour. In DWH, grackles were approximately as numerous as they were during unprovisioned observations at StJ (2.3 per scan).

The end result of differences in aggression rates and individuals per species for the two areas is illustrated in Figure 2. In StJ, the random sample of scans for each trial indicates that Zenaida doves foraged most often alone in unprovisioned trials (89% of scans), whereas in provisioned trials doves foraged alone (48% of scans), or a single dove foraged close to one or more grackles (38% of scans); in contrast, at DWH they fed close to a conspecific in most

trials (72% of scans), $\chi^2(6, N = 300) = 205.10, p < .001$ (among the three distributions), and close to grackles only on a small proportion of scans (9%).

Overall, the field results indicate, first, that Zenaida doves from StJ and DWH forage under very different conditions, with the former feeding most often away from conspecifics and showing relatively high levels of intraspecific aggression. In contrast, DWH doves forage in large flocks and show much less intraspecific aggression per individual. Second, Carib grackles are the most frequent foraging associate of Zenaida doves in StJ, whereas conspecifics represent the most frequent associate at DWH; interspecific aggression against grackles is rare or nonexistent in both areas, even though provisioning with rice attracts large numbers of grackles at sites in StJ. Finally, populations of Zenaida doves from StJ and DWH show clear quantitative differences in social foraging: Zenaida doves from StJ feed most often alone or with heterospecifics, using interference competition against conspecifics and scramble competition against birds of other species. In contrast, doves from DWH feed with conspecifics and predominantly use scramble competition when foraging with other doves and, more rarely, with birds of other species. Clear differences therefore exist in social foraging of Zenaida doves with conspecifics and with Carib grackles at the StJ and DWH areas. The experiments reported in the following section tested in captivity the social learning differences related to these social foraging differences in the field.

Captive Experiments

General Method

Subjects and Maintenance

For the captive study, 73 Zenaida doves (51 from StJ and 22 from DWH) and 3 grackles were caught in walk-in traps. Individ-

Table 2

Mean Number of Birds per Site for the Six Species Seen, as Well as Frequency and Rate of Intraspecific and Interspecific Aggression Involving Zenaida Doves

| Site	Zenaida dove	Carib grackle	Lesser Antillean bullfinch	Glossy cowbird	Ground dove	Feral pigeon
St. James: unprovisioned						
Birds per site (M)	3.6	2.6	0.5	0.1	0.3	0.0
No. of aggressive acts	468	10	0	0	0	0
Rate per dove per hour	7.7	0.2	0.0	0.0	0.0	0.0
St. James: provisioned						
Birds per site (M)	1.2	7.9	0.2	0.3	0.1	0.0
No. of aggressive acts	1,374	17	0	0	0	0
Rate per dove per hour	76.3	0.9	0.0	0.0	0.0	0.0
Deep Water Harbour						
Birds per site (M)	66.9	2.3	0.6	1.4	0.1	3.3
No. of aggressive acts	267	0	0	0	0	0
Rate per dove per hour	1.2	0.0	0.0	0.0	0.0	0.0
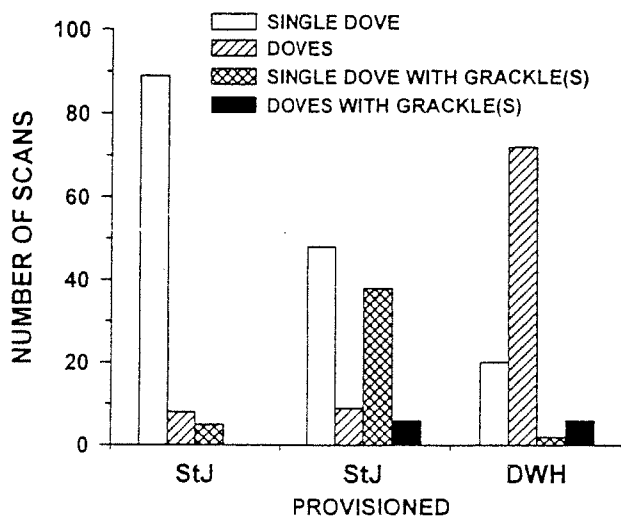
Figure 2. One hundred randomly chosen scans showing the probability of Zenaida doves foraging alone, with other doves, alone with grackles, or with other doves and grackles in St. James without provisioning (StJ), in St. James with provisioning (StJ PROVISIONED), and at the Deep Water Harbour (DWH).

uals were identified with colored leg bands and held in captivity for at least 1 week before testing. Birds were housed and tested individually in wire mesh cages (30 cm^3) kept in a 2.7 × 4.8 × 2.7 m^3 outdoor aviary at the Bellairs Research Institute of McGill University in StJ. Testing of each subject took place in an enclosed section of the aviary, out of visual contact with the other doves. Before testing, doves were fed an ad libitum mixture of commercial mixed finch seed, cracked corn, lentils, and cooked white rice. Grackles were fed cooked rice and mynah pellets. At the end of the captive study, all doves and grackles were fed to satiation and released near their site of capture.

Experimental Procedure

The captive studies all involved three phases of experimentation: tutor training, tutor–observer demonstrations, and observer testing. Dove and grackle tutors from each location were progressively shaped to perform the experimental task. In all three studies, grackles were found to consistently learn the novel task faster than the doves. Once all tutors had equally short feeding latencies (<10 s), 1 grackle and 1 dove tutor were placed adjacent to one another, 30 cm in front of an observer's cage that was positioned directly opposite the midline separating the tutors' cages. The front of both the tutor and observer cages had openings allowing access to the experimental task. The tutors had no visual contact with each other during trials or with the observer during testing; the experimenter observed all trials from behind a blind. Each new subject was placed in the experimental setup the day before the experiment and deprived of food overnight. This ensured that the birds were sufficiently motivated and habituated to the tutors before each session. Each trial consisted of one 5-min demonstration and one 5-minute observer test with a 1-min interval between trials. All sessions were conducted between 10:00 a.m. and 2:00 p.m.

Experiment 1: Novel Food Choice (StJ)

Method

Tutor training. Three doves and 3 grackles caught in StJ were trained as tutors. The novel food consisted of cooked white rice, colored either red or green with commercial food dye. The novel foods, mixed with plain rice, were presented to both dove and grackle tutors. Dove tutors initially showed a striking tendency to eat white rice only, selectively picking out the undyed kernels from the dyed ones. They eventually picked up kernels of dyed rice and habituated to feeding on either color in the absence of white rice.

Experimental design. Eighteen doves were assigned to one of two control groups and 30 doves to one of two experimental groups. On the basis of the high level of interspecific aggression revealed in the field study, Control Group 1 ($n = 12$) was used to examine the possibility that dove tutors could selectively inhibit or threaten conspecifics to avoid either the food or the side of the cage that was closest to it. On 2 consecutive days, birds from this group were presented with two dishes, placed side by side outside their cage and adjacent to the holes through which normal maintenance feeding was done. The dishes contained identical amounts and type of a food the doves were familiar with: 10 g mixed finch seed on Day 1 and 10 g cooked white rice on Day 2. On each of these days, two trials were conducted in which the right–left position of the conspecific and heterospecific was reversed between Trial 1 and Trial 2 and any food eaten during the first trial was replenished for the second one. In this control group, we noted the dish from which the dove ate during its first feeding bout per trial and every 30 s, we also noted the position of the dove inside its cage (right half vs. left). On a continuous basis, we recorded any threat displays (ritualized beak swipes at the ground or raising of the wing) or attempted attacks (pecks or wing slaps) directed to either the conspecific or the grackle. During these trials, the conspecific and the heterospecific were deprived of food and had no food in front of their own cages.

In Control Group 2 ($n = 6$), we examined any spontaneous tendency to eat dyed rice in the absence of tutor information. On 2 consecutive days, birds from this group were given 10 daily trials with a dish containing red rice and one containing green rice placed outside their cage near the holes used for normal maintenance feeding. Each trial was conducted in the presence of 2 food-deprived birds, a conspecific and a heterospecific, that had no food in front of their cages.

Zenaida doves from the experimental groups were given a demonstration of a conspecific and heterospecific tutor eating the novel food before their choice test. Fifteen doves were given a demonstration of a conspecific eating red rice and a grackle eating green rice out of a petri dish. Another 15 naive doves observed the reverse. Left–right position of the tutor types with respect to the observer was randomly varied. After each demonstration, the naive dove was presented simultaneously with the two colors of rice, each offered on the same side of the cage as its tutor. A preference was determined when a naive dove ate from one of the dishes of colored rice. Once a choice was made, the food was immediately removed and the trial repeated to test for stability of choice; our measure of choice therefore reflects the potential influence of the tutor, without allowing the observer to gain individual experience with the food types through prolonged consumption. Each subject was given a maximum of 10 trials a day for 5 consecutive days.

Results and Discussion

None of the doves in any of the groups performed threat displays or attempted to attack the conspecific or the grackle during either the experiments or normal housing and maintenance. In all groups, tutor, control, and observer birds of both species fled to the back of their cage when the experimenter approached to place the feeding apparatus in front of them, thereby modifying the position and orientation held during pretest conditions (control or demonstration); birds returned to the front of the cage only once the experimenter was hidden behind the blind. Birds from Control Group 1 showed no tendency to avoid or prefer the dish or side of their cage closest to the conspecific. For both types of familiar food, doves from this group ate, stood, or rested in the half of their cage that was closest to the grackle on 4.6 of the 10 scans conducted per trial and in the half closest to the dove tutor on 5.4 scans. A Food Type × Trial analysis of variance (ANOVA) revealed no significant effects of either variable on spatial position with respect to tutor species. $Fs(1, 11) = 0.59$ for food type, 0.04 for trial, and 0.76 for interaction, all ns. In the 38 trials in which the 12 subjects fed (of a possible total of 48), the dish that was first eaten from was on the grackle tutor's side in 21 cases (10 trials with seed and 11 trials with white rice) and on the dove tutor's side in 17 cases (8 trials with seed and 9 trials with white rice), $\chi^2(1, N = 18) = 0.67$ for species effect and $\chi^2(1, N = 20) = 0.63$ for seed and white rice, both ns.

Overall, birds from Control Group 2 showed no spontaneous tendency to eat dyed rice: Only 1 of the 6 birds ate the colored rice by the 20-trial ceiling. In contrast, all 30 birds in the experimental groups had eaten by Trial 13; this difference between tutored and untutored individuals was significant at the .001 level. Yates corrected $\chi^2(1, N = 36) = 22.48$. Of the 30 tutored doves, 20 chose the color of rice eaten by the grackle tutor on their first 2 trials, whereas 8 chose the color eaten by the dove tutor (Figure 3). Two doves made unstable choices (i.e., changed from their first to their second feeding trial). Expected frequencies for each of the three response categories were determined from joint
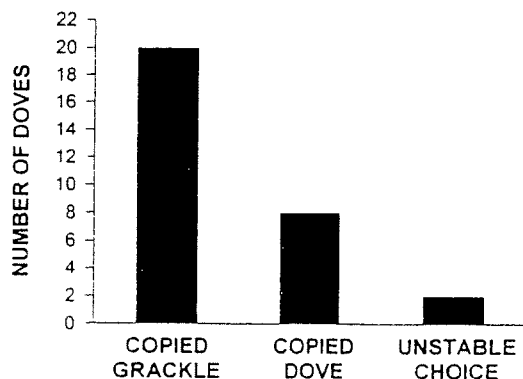

Figure 3. Number of Zenaida doves that chose the same food type as the grackle or dove tutor on two consecutive choices. An unstable choice indicates choosing the foods eaten by different tutors on the two trials.

random probabilities (a .5 chance of learning from either tutor on Trial 1 and .5 chance of doing so on Trial 2, which yielded a .25 joint probability over 2 trials; the unstable choice probability was .5, from a .25 chance of choosing a dove and then a grackle plus a .25 chance of choosing a grackle and then a dove). A significant difference was found between observed and expected frequencies in a chi-square analysis. Yates corrected $\chi^2(1, N = 30) = 32.13, p < .001$. When only the first choice was considered, the results also showed a significant bias toward the food type eaten by the grackle (21 vs. 9), $\chi^2(1, N = 30) = 4.03, p < .05$. No significant preference was shown for a particular food color independently of the tutor type eating it, $\chi^2(1, N = 30) = 0.84$, ns. Latency to eating, measured by the number of demonstrations the observer required before first eating the food, did not differ between doves that chose the same food as did the grackle tutor ($M = 4.1$ trials, $SE = 0.9$) and the dove tutor ($M = 3.3$ trials, $SE = 1.1$), $F(1, 28) = 0.29$, ns.

The trend toward eating the same food type as the grackle occurred regardless of tutor differences in rates of pecking. In 10 randomly chosen observer–tutor pairings, observational counts of pecking rates showed that 7 doves saw a dove tutor eating more rapidly than a grackle tutor, yet 6 of them still chose the grackle. In the remaining 3 cases, the grackle tutor was observed to eat more rapidly than the dove tutor, and all 3 observer doves chose the food eaten by the grackle. On their first encounter with a novel food type, Zenaida doves from StJ clearly appeared to choose the type eaten by a heterospecific tutor.

Experiment 2: Novel Food-Finding Technique (StJ)

Method

Apparatus. In the second experiment, the doves were required to learn a novel task: pushing a lid off an opening in a box to reveal mixed seed and cooked white rice inside. The lid was a black plastic, twist-off jar cover 5.5 cm in diameter and 1 cm high. The box was constructed out of pressboard and measured $7 \times 7 \times 3.5$ cm^3 with a hole (1 cm deep) in the top 5 cm in diameter. Tutor identity, housing conditions, feeding schedules, and experimental setup were the same as in Experiment 1.

Tutor training. The same tutors from Experiment 1 were trained to push the lid off the box by starting with the lid partly covering the food and then progressively covering the entire hole. The naive doves were allowed to habituate to the food box for an average of 2 days before the experiment by having their food presented in the box without the lid.

Experimental design. During the demonstration phase, one tutor pushed a lid off and fed from a box while the other tutor fed from an open petri dish (5.5 cm in diameter and 1 cm high). Twenty-two Zenaida doves were tested as observers in this experiment; the birds represented a randomly chosen subset of the 30 used in the experimental groups of Experiment 1. Of the 22 doves tested, 11 observed a grackle tutor pushing a lid and a dove eating from the open control dish and 11 observed the reverse. In each demonstration, the tutor with the box could only push the lid once and eat from the box, whereas the other tutor simultaneously ate from the control dish.

The naive dove was then offered a choice between a lid-covered box and an empty open dish, arranged to coincide with the side of

their tutors. Observers were given a maximum of 10 trials a day for 5 consecutive days. Testing was terminated if an observer succeeded in removing the lid and eating on 2 consecutive trials. In addition, any pecks at the empty control dish were recorded for each observer dove. No untutored birds were run in this experiment, because the task was identical to the one used in previous studies: in the absence of a tutor, naive Zenaida doves have a very low probability of spontaneously removing an opaque lid covering hidden food (1 bird out of 16; Lefebvre et al., in press; see also Experiment 3).

Results and Discussion

As in Experiment 1, both observers and tutors fled to the back of their cage when the experimenter approached to place the feeding apparatus in front of them, modifying the position and orientation held during the demonstration; birds returned to the front of the cage only once the experimenter was hidden behind the blind. The results from Experiment 2 are illustrated in Figure 4. Of the 11 doves that observed a grackle tutor push the lid and eat, 7 learned the task; only 1 dove out of 11 learned after observing a dove demonstrate the task. In tests with a 2 × 2 contingency table, there was a significant relationship between the number of doves that learned to eat from the box and the tutor they learned from, $\chi^2(1, N = 22) = 4.92, p < .05$. When the 50-trial ceiling value was assigned to the 4 grackle-tutored and 10 dove-tutored birds that failed to remove the lid, latency to opening was significantly shorter in grackle-tutored observers than in dove-tutored ones (one-way ANOVA), $F(1, 20) = 7.88, p < .011$ (data were transformed by the reciprocal to normalize the ceiling effect). When birds that failed to open were excluded from the analysis, the latency to opening of the only dove-tutored observer that removed its lid (on Trial 15) was well within the range of the 7 grackle-tutored openers (M number of trials to opening $= 12.7, SE = 6.2$). As in Experiment 1, tutor type therefore seemed to influence the probability of learning from a particular tutor rather than the latency to learning. More surprisingly, grackle tutors seemed to influence observers even when they provided inappropriate information. The right side of Figure 4 represents the number of doves that pecked at the empty control dish instead of the lid covering the food. When a dove tutor was removing the lid and a grackle tutor was eating from an open control dish, 5 doves pecked at the empty control dish. When the tutors were reversed and a dove tutor was eating from an open control dish, no doves pecked at their empty dish. There was a significant relationship between the number of birds that pecked at the empty dish and the tutor they observed eating from a similar open dish, $\chi^2(1, N = 22) = 10.05, p < .01$. As in Experiment 1, observer doves therefore directed their foraging behavior toward stimuli that most closely resembled the stimuli their grackle tutor interacted with; even though grackle-tutored doves could never obtain food from the open control dish, several of them not only pecked at the dish in the absence of any seed but also failed to learn the alternative, dove-demonstrated technique of removing the lid. In this group, such a trend was all the more surprising given that the observer's apparatus was visually identical to the one in which the dove tutor obtained food (a box with a black lid) but different from the one in which the grackle tutor did (an open dish that contained seed for the tutor but no seed when later given to the observer). When tutor assignment was reversed, Zenaida dove observers never touched the empty dish similar to the one in which the conspecific tutor had eaten earlier but learned instead to remove the lid on the box from which the grackle tutor ate.

Experiment 3: Novel Food-Finding Technique (DWH)

Method

Apparatus. Similar to the apparatus in Experiment 2, the novel task consisted of pushing a lid off an opening (5 cm in diameter and 1 cm deep) in a wooden block (10 × 5 × 5 cm³) and eating two grains inside. The grains were lentils for the dove tutor and mynah pellets (similar in size and appearance to lentils) for the grackle. The lid was an inverted plastic petri dish (5.5 cm in diameter and 1 cm high) covered with masking tape.

Tutor training. One dove caught in DWH and 1 grackle caught in StJ were trained to open the lid as in the previous experiment. The tutors had a maximum of 1 min to perform. In almost all cases, both birds performed within 10 s; mean latencies ($\pm SD$) were 7.0 $\pm$ 2.6 s for the dove and 5.3 $\pm$ 3.5 s for the grackle, $t(14) = 1.12, ns$.

Experimental design. During the demonstration phase, one tutor performed the novel task while the other simultaneously fed from the petri dish. Of the 21 doves tested, 8 were randomly assigned to the dove-tutored group and 8 were randomly assigned to the grackle-tutored group. Doves in the former group observed the dove demonstrating the novel task and the grackle feeding from the petri dish; doves in the latter group observed the opposite combination. The remaining 5 control doves observed each of the 2 tutors presented with an empty apparatus for 1 minute (lid opened); neither tutor touched its apparatus in this condition. In each group, the grackle tutor was on the left side for 4 of the subjects and on the right side for the other 4. For control birds, the grackle was on the left for 3 of the 5 subjects.

After the demonstration, the subject was offered a choice between a lid-covered box and an empty petri dish placed adjacent to
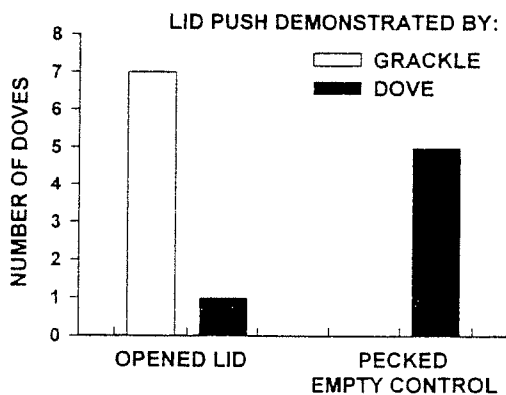

Figure 4. Number of Zenaida doves from St. James that learned the novel lid-opening task or pecked at the control dish as a result of the species demonstrating the novel task.

one another. For half of the subjects, the lid was on the same side as the lid tutor; for the other half, it was on the opposite side. In the control condition, the observer's lid was on the same side as the tutor's for 3 of the 5 subjects. Observers were given 10 trials a day for 4 consecutive days. An observer was classified as having learned the novel task if it pushed the lid and ate on 2 consecutive trials. In addition to lid pushing, pecks at the empty dish were recorded for each dove.

Results and Discussion

Birds again fled to the back of their cage when the experimenter approached to place the feeding apparatus and returned to the front of the cage only when the experimenter was hidden behind the blind. Of the 8 doves that observed a dove demonstrate the novel task, 7 learned this task. In contrast, none of the doves that observed a grackle performing the same novel task learned it (Figure 5). Thus, the identity of the tutor had a significant effect on the ability of the doves to learn the novel task (Fisher exact test: $p <$ .001). None of the 8 doves in the dove-tutored group pecked at the empty petri dish. However, when a dove control ate from the open dish, 1 of the 8 observers in the grackle-tutored group did, in fact, peck at the empty dish, although the effect was not significant. None of the control, untutored doves performed either the novel task or the alternative task.

Of the 7 birds that learned, all did so by the 16th trial ($M = 7.9$ trials, $SD = 6.5$). Three of these individuals performed the novel task correctly on the very 1st trial.

General Discussion

We have shown that territorial Zenaida doves, which exhibit interference competition with other doves and scramble competition with Carib grackles, learned more readily the food choice and food-finding technique of a heterospecific tutor. In contrast, doves from a gregarious population, which scramble compete with other doves, showed the reverse tutor preference, learning a novel task more readily from a conspecific than from a heterospecific

tutor. Within the constraints of our methodological assumptions, these findings suggest that social learning pathways in Zenaida doves are flexible rather than species specific and that foraging interactions observed in the field can be used to predict the direction of social learning that will be exhibited in a controlled setting. Further experiments may be needed to generalize these results beyond the limits of our procedure, but several arguments support our assumptions on the effects of tutor species and field interactions. In the field, grackles are as numerous at DWH (2.3 per scan) as they are at StJ (2.6 per scan in unprovisioned trials) and scramble compete with Zenaida doves at both sites; the major difference between the sites therefore lies in the number of doves that feed together and the mode of intraspecific foraging competition. In Experiment 3, the grackle tutor did not differ from the dove tutor in latency to opening the lid-covered apparatus; species identity, not relative efficiency of the individuals trained for tutoring, is therefore the most plausible explanation for the differential tutor effect seen in our captive study.

Taken together, the results presented here support our hypothesis that scramble competition, rather than group living, may be a major determinant behind the social learning of foraging behavior. This hypothesis predicts that preferential routes of social learning will be seen not in terms of species identity (i.e., conspecific vs. heterospecific) but in terms of the mode of foraging competition (scramble vs. interference competition). The modes of foraging competition exhibited by a species should, in turn, depend directly on the ecological characteristics of its foraging environment and resource defendability (Brown, 1964; Emlen & Oring, 1977).

Foraging Ecology and Modes of Foraging Competition

The distribution of resources in time and space and the density of animals competing for these resources play a role in determining whether a species will exhibit scramble or interference competition for food (Davies & Houston, 1984). Brown's (1964) theory of economic defendability holds that a forager should only defend an area for which the difference between the energetic benefits gained and costs incurred is greatest; benefits increase with the number of resource items available, and costs increase with the number of competitors present. In general, resource items that are uniformly distributed and continuously renewed are much more defendable than patchily distributed resource items that occur unpredictably (Grand & Grant, 1993; Horn, 1968). Thus, large amounts of high-quality food arriving unpredictably in time and space tend not to be defended, in part because such resource patches attract such a large number of competitors that they would be too costly to defend (Davies & Houston, 1984). In addition, when many resource items are available synchronously, any time spent defending the resource would simply take away from time spent feeding (Grant & Kramer, 1992).

At DWH, several factors act together to create a foraging resource that may be economically undefendable. Not only
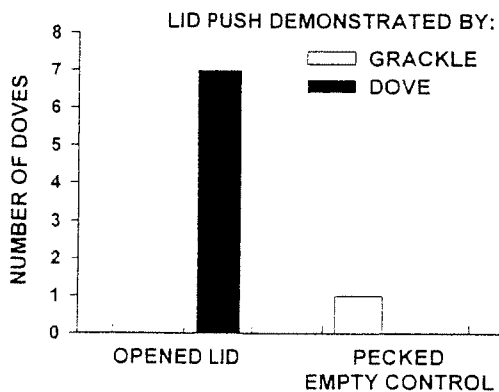

LID PUSH DEMONSTRATED BY:
☐ GRACKLE
■ DOVE

Figure 5. Number of Zenaida doves from the Deep Water Harbour that learned the novel lid-opening task or pecked at the control dish as a result of the species demonstrating the novel task.

are large quantities of food items (cereal and legumes) available unpredictably and synchronously via different delivery shoots, but the frequent interruptions of feeding by human activity and by the removal of spilled grain generate a situation in which the resource is essentially ephemeral. Hence, the depletion of resources is independent of the number of competitors present. In this foraging environment, Zenaida doves are present in large numbers, exhibit low rates of intraspecific aggression relative to those exhibited by territorial doves, and scramble compete in dense clusters at point sources of food arrival in much the same manner as do feral pigeons in the port of Manchester (Murton et al., 1972).

In contrast, the coastal populations exhibit the territoriality and interference competition considered to be more typical of Zenaida doves (Bond, 1985; Devas, 1970; Goodwin, 1983). Intraspecific aggression rates are high at both natural and provisioned sites, and doves forage most commonly either alone or in mated pairs, with family groups of three or four birds occasionally being observed in the dry season. This type of social behavior is consistent both with the region's sparse and more uniformly distributed food items, which consist mainly of the seeds of grasses and fruits, as well as fallen fruits (Lack, 1976), and with the arboreal vegetation that the doves defend for roosting and nesting sites. Such vegetation is noticeably lacking from the harbor area, where up to 50 doves can be seen roosting in the single small tree present.

Adaptive Specialization or Learned Adjustment to Local Conditions?

At the interspecific level, adaptive theories of learning usually assume that a match between variation in ecological conditions and variation in learning patterns is based on natural selection of genetically based learning specializations. In the present study, a similar match between ecology and learning was found at the intraspecific level. We have shown that two populations of the same species that differ in their social organization use different social learning pathways to acquire the same novel foraging information and that the pathway used depends ultimately on the population's foraging ecology.

The present results suggest that variation in resource defendability can lead to variation in competitive foraging interactions in mixed or homospecific flocks, which in turn can lead to variation in the direction of social learning. Because we have no evidence for genetic differences between our Zenaida dove populations, learning schedules in the different habitats may well have brought about the differences revealed by our social learning experiments: different stimulus–response and reinforcement contingencies may be present in the two environments. This raises the interesting possibility that even when comparative experiments feature different species, environmentally determined contingencies may underlie interspecific differences, just as they underlie the interpopulation differences reported here. Only adequate experimental transplants between the terri-

torial and gregarious populations will allow us to determine whether individual experience does indeed affect the development of social learning pathways. For instance, transplanting marked juvenile and adult doves from StJ to the DWH site and vice versa would allow us to determine whether the preferred learning pathway becomes established at an early age or whether it is flexible and dependent only on recent foraging experience.

Heterospecific Versus Conspecific Tutors

There is no reason, a priori, to expect an animal to learn more easily from a heterospecific than from a conspecific. Logically, conspecifics should be more informative tutors because they have more similar motor capacities and diets. Different species will seldom overlap perfectly in the food types they eat and may be capable of motor acts that are irrelevant or difficult for a naive heterospecific to perform. Indeed, Klopfer (1961) proposed that interspecific imitation should be rare in mixed-species groups with distinct foraging techniques. In the case of Zenaida doves and Carib grackles, these differences can be quite pronounced. Grackles are omnivorous, with a diet ranging from plant to animal matter, including insects and lizards, as well as food scraps left by humans (Ffrench, 1973; Stamps, 1983). In contrast, Zenaida doves are predominantly granivorous and do not use the variety of fine beak manipulations and probing movements of which grackles are capable.

Observing a heterospecific tutor would necessarily involve filtering out of irrelevant information about both food and behavior. This added cost of information filtering must therefore be weighed against the lower cost of aggression or the higher value of foraging information, or both, to determine whether learning should preferentially focus on heterospecifics or conspecifics. The fact that territorial Zenaida doves do prefer heterospecific over conspecific tutors suggests that intraspecific aggression rates may be high enough to outweigh the cost of information filtering. However, it should be emphasized that, in our experiments, the apparatus was constructed in such a way that both grackle and dove tutors were forced to use very similar techniques (pushing or pecking the lid aside) that were relatively easy for the dove observers to perform. If we had changed either the nature of the food reward given to tutors (e.g., a food type not normally eaten by doves) or the nature of the food-finding technique (e.g., an open-beak probing behavior that doves never use), our results could conceivably have been quite different. Strictly speaking, therefore, the present study was not a test of Klopfer's (1961) proposal that interspecific learning will be rare between species with distinct foraging techniques. Only a comparison between observer-relevant and observer-irrelevant demonstrations by heterospecific tutors can offer direct evidence for or against Klopfer's predictions.

If the scramble competition hypothesis correctly accounts for social learning pathways, then animals that scramble compete against both conspecifics and heterospecifics should learn as readily from their own species as they do

from the other one. Experimental support for this prediction, using different tutor techniques species typical of either grackles or doves, has recently been obtained with a coastal Carib grackle population that scramble competes with both conspecifics and territorial *Z. aurita* (Lefebvre, Brown, Koelle, & Templeton, 1995).

References

Altmann, J. (1989). The monkey and the fig. *American Scientist, 77,* 256–263.

Balda, R. P., & Kamil, A. C. (1990). A comparative study of cache recovery by three corvid species. *Animal Behaviour, 38,* 486–495.

Bond, J. (1985). *Birds of the West Indies* (5th ed.). London: Collins.

Brown, J. L. (1964). The evolution of diversity in avian territorial systems. *Wilson Bulletin, 76,* 160–169.

Caribbean Meteorological Institute. (1982). *Averages and extremes of meteorological elements, No. 2.* Husbands, Barbados: Author.

Davies, N. B., & Houston, A. I. (1984). Territory economics. In J. R. Krebs & N. B. Davies (Eds.), *Behavioural ecology: An evolutionary approach* (pp. 148–169). Oxford, England: Basil Blackwell.

Devas, R. P. (1970). *Birds of Grenada, St. Vincent, and the Grenadines.* St. Georges, Grenada: Carenage Press.

Domjan, M., & Galef, B. G. Jr. (1983). Biological constraints on instrumental and classical conditioning: Retrospect and prospect. *Animal Learning and Behavior, 11,* 151–161.

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science, 197,* 215–223.

Ffrench, R. (1973). *A guide to the birds of Trinidad and Tobago.* London: Macmillan.

Gandolfi, G. (1975). Social learning in non-primate animals. *Bollettino di Zoologia, 42,* 311–329.

Goodwin, D. (1983). *Pigeons and doves of the world* (3rd ed.). Ithaca, NY: Cornell University Press.

Grand, T. C., & Grant, J. W. A. (1993). Spatial predictability of food influences its monopolization and defence by zebrafish, *Brachydanio rerio. Animal Behaviour, 47,* 91–100.

Grant, J. W. A., & Kramer, D. L. (1992). Temporal clumping of food arrival reduces its monopolization and defence by zebrafish, *Brachydanio rerio. Animal Behaviour, 44,* 101–110.

Haverschmidt, F. (1969). The Zenaida dove on Barbados. *Ibis, 111,* 613.

Horn, H. S. (1968). The adaptive significance of colonial nesting in the Brewer's blackbird *(Euphagus cyanocephalus). Ecology, 49,* 682–694.

Hutt, M. B. (1979). *Barbadian nature diary.* Bedford, Nova Scotia, Canada: Layne.

Kamil, A. C. (1988). A synthetic approach to the study of animal intelligence. In D. W. Leger (Ed.), *Comparative perspectives in modern psychology* (pp. 257–308). Lincoln: University of Nebraska Press.

Klopfer, P. H. (1959). Social interactions in discrimination learning with special reference to feeding behavior in birds. *Behaviour, 14,* 282–299.

Klopfer, P. H. (1961). Observational learning in birds: The establishment of behavioural modes. *Behaviour, 17,* 71–80.

Krebs, J. R., Healy, S., & Shettleworth, S. J. (1990). Spatial memory of Paridae: Comparison of a storing and a non-storing species, *Parus ater* and *Parus major. Animal Behaviour, 39,* 1127–1137.

Krebs, J. R., MacRoberts. M. H., & Cullen, J. M. (1972). Flocking and feeding in the great tit *Parus major:* An experimental study. *Ibis, 114,* 507–530.

Lack, D. (1976). *Island biology, illustrated by the land birds of Jamaica.* Los Angeles: University of California Press.

Lefebvre, L., Brown, K., Koelle, M., & Templeton, J. (1995). *Imitation in Carib grackles learning from conspecifics and from Zenaida doves.* Manuscript in preparation.

Lefebvre, L., & Giraldeau, L.-A. (in press). Is social learning an adaptive specialization? In B. G. Galef, Jr., & C. M. Heyes (Eds.), *Social learning in animals: The roots of culture.* New York: Academic Press.

Lefebvre. L., Palameta, B., & Hatch, K. K. (in press). Is group-living associated with social learning? A comparative test of a gregarious and a territorial Columbid. *Behaviour.*

Lévesque, H., & McNeil, R. (1986). Déplacements du pigeon biset *(Columba livia)* dans le Vieux-Port de Montréal [Feral pigeon *(Columba livia)* movements in the Old Port of Montreal]. *Naturaliste Canadien, 113,* 47–54.

Murton, R. K., Coombs, C. F. B., & Thearle, M. J. B. (1972). Ecological studies of the feral pigeon *Columba livia* var. II: Flock behavior and social organization. *Journal of Applied Ecology, 9,* 875–899.

Palameta, B. (1989). *The importance of socially-transmitted information in the acquisition of novel foraging skills by pigeons and canaries.* Unpublished doctoral dissertation. Cambridge University. Cambridge, England.

Pinchon, R. (1963). *Faune des Antilles francaises: les oiseaux [Fauna of the French West Indies: Birds].* Fort-de-France, Martinique: Muséum d'histoire naturelle.

Rozin, P. R., & Kalat, J. W. (1971). Specific hungers and poison avoidance as adaptive specializations of learning. *Psychological Science, 4,* 179–184.

Sasvari, L. (1979). Observation learning in great, blue, and marsh tits. *Animal Behaviour, 27,* 767–771.

Sasvari, L. (1985). Different observational learning capacity in juvenile and adult individuals of congeneric bird species. *Zeitschrift für Tierpsychologie, 69,* 293–304.

Sherry, D. F., & Schacter, D. L. (1987). The evolution of multiple memory systems. *Psychological Review, 94,* 439–454.

Shettleworth, S. J. (1993). Where is the comparison in cognitive cognition? Alternative research programs. *Psychological Science, 4,* 179–184.

Stamps, J. (1983). The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard *(Anolis aeneus). Behavioral Ecology and Sociobiology, 12,* 19–33.

Strupp, B. J., & Levitsky, D. E. (1984). Social transmission of food preferences in adult hooded rats *(Rattus norvegicus). Journal of Comparative Psychology, 98,* 257–266.