

CARIB GRACKLES IMITATE CONSPECIFIC AND ZENAIDA DOVE TUTORS

by

LOUIS LEFEBVRE, JENNIFER TEMPLETON¹⁾, KATHLEEN BROWN and
MICHELLE KOELLE²⁾

(Department of Biology, McGill University, Montréal, Québec, H3A 1B1, Canada)

(Acc. 27-III-1997)

Summary

In Barbados, Carib grackles (*Quiscalus lugubris*) forage in opportunistic aggregations that include territorial Zenaida doves (*Zenaida aurita*) and flocks of conspecifics. In searching for and handling food, grackles use complex beak movements and modulate priority of access with a mixture of postural signals and intra- and interspecific scramble (unaggressive) competition. We show in two experiments that wild-caught grackles learn as readily from a Zenaida dove as they do from a conspecific tutor, whether tutors use similar or different food-finding techniques. Grackles also imitate the technical variant that the hetero- and conspecific tutors were shaped to demonstrate: those who observed a Zenaida dove used the dove's closed beak pecking technique, while those who observed a conspecific used the grackle's open beak pulling, probing or prying. Our findings suggest that imitation, like other forms of social learning, is strongly influenced by a species' foraging ecology. In particular, the ability to imitate novel motor skills should be favored in opportunistic species which exhibit scramble competition and which use complex searching and handling techniques to forage on embedded foods.

Introduction

Imitation is the copying by a naive observer of the motor act of a knowledgeable tutor. It is a form of response (as opposed to stimulus) learning (Heyes, 1993) and is thought to be a key step in the continuum linking

¹⁾ Present address: Department of Biology, Bowdoin College, Brunswick, Maine 04011, USA.

²⁾ This work was funded by a grant from NSERC to LL and a Commander Bellairs Post-doctoral Fellowship to JT.

simple forms of culture (Kawai, 1965; Bonner, 1980) with the more complex ones seen in humans (Whiten, 1993; Russon *et al.*, in press). Too few species have been tested up to now for a comparative synthesis of imitation to be possible (Heyes, 1993), but specific predictions based on a species' foraging ecology may be made concerning both the capacity to imitate food finding techniques and the species from which the techniques could be learned.

Opportunistic foragers that use both complex food searching and handling techniques and scramble competition (non-aggressive foraging interactions; Grant, 1993) are likely to be prime candidates for imitation (Russon *et al.*, in press). The use of complex motor acts for the discovery and extraction of food is a logical correlate of imitation; Parker (1996) has proposed that dietary specialization on embedded foods may have favored imitation as a way to master complex extraction techniques in great apes. In addition, dietary opportunism (Klopfer, 1961; Sasvari, 1985; Lefebvre & Giraldeau, 1996) and the 'mental arms race' (Palameta, 1989) that favours rapid feeding in the presence of scramble competitors have both been empirically linked to social learning. In particular, previous research on three, ecologically different populations of Zenaida doves (*Zenaida aurita*) has demonstrated that doves learn most readily from the birds they scramble compete with, whether these are heterospecifics in a territorial population, conspecifics in a group-foraging population (Dolman *et al.*, 1996) or hetero- and conspecifics in a mixed population (Carlier & Lefebvre, in press).

In this paper, we propose that the Carib grackle of Barbados (*Quiscalus lugubris*) is a good candidate for both intra- and interspecific imitation. Carib grackles forage in small, mobile flocks and are gregarious, urbanized opportunistic-generalists throughout their range (Lesser Antilles and northern South America: Ffrench, 1973; Voous, 1983). When foraging on hidden or embedded foods, grackles use their beak to push aside or tear obstacles, to probe for covered items and to kill animal prey (*e.g.* insects, lizards: Ffrench, 1973); when removing food from the substrate, they are capable of fine movements of the beak and head, often using their feet for leverage and holding of the food item (unpubl. obs.). To deal with intraspecific competitors, Carib grackles use a mixture of scramble competition (rapid, unaggressive ingestion) and ritualized signaling (vocalizations and head postures) to modulate priority of access to food (unpubl. obs.).

In Barbados, they also often associate in mixed species aggregations with territorial *Zenaida* doves. Territorial *Z. aurita* are extremely aggressive against conspecific intruders, but grackles and doves show little or no aggression towards each other, using scramble competition when they interact over food (Carlier & Lefebvre, 1996; Dolman *et al.*, 1996). Based on this foraging ecology, we predict that: 1) Carib grackles will be equally likely to learn from a *Zenaida* dove tutor as they are to learn from a conspecific one; and 2) Carib grackles will be capable of imitating the specific motor technique used by a pre-trained tutor.

In evaluating imitation, it is essential for experimental designs to control for simpler stimulus processes (Galef, 1988; Visalberghi & Fragaszy, 1990; Whiten & Ham, 1992). When an observer sees a demonstrator use a new response to interact with environmental cues, the most likely confound for response imitation lies in these cues, either in the form of local or stimulus enhancement (increased attention to the cues; Thorpe, 1963) and/or stimulus learning (pairing of the cues with the reward obtained by the demonstrator, Heyes, 1993; or, of the cues with an innate social releaser, Suboski, 1990). Few experimental designs effectively control for these stimulus confounds (Palameta & Lefebvre, 1985). The most effective one involves different motor solutions to the same feeding problem (Heyes, 1996; Whiten & Custance, 1996; Zentall, 1996): some observers see a tutor using one motor variant, other observers see a second variant. The variants must be equally novel and improbable, they must involve identical environmental cues, and must lead with equal efficacy to the reward. In a post-observation test where the variants are equally feasible and where environmental cues are sometimes changed to prevent animals from relying on them (Heyes *et al.*, 1992), observers are then expected to show the variant they saw their particular demonstrator use. Experiments on budgerigars (Dawson & Foss, 1965; Galef *et al.*, 1986), rats (Heyes *et al.*, 1992), pigeons (Zentall *et al.*, 1996), quail (Akins & Zentall, 1996) and chimpanzees (Whiten *et al.*, 1996) have all obtained positive results using this procedure.

In this study, we first provide Carib grackles with either a conspecific or a heterospecific (*Zenaida* dove) tutor and show that grackles learn as readily from either one, consistent with the scramble competition they exhibit with both species in the field. We then show that learning from either tutor type

occurs whether the latter are shaped to use similar food-finding techniques or allowed to perform different, species-typical, movements; these options respectively control for type 1 and 2 error in the study. In addition, we show that grackle observers use the same motor variant their tutor demonstrated in opening its feeding apparatus, whether the tutor is a conspecific or a Zenaida dove.

Experiment 1: Similar tutor techniques

In experiment 1, we provide naive observer grackles with conspecific or heterospecific tutors shaped to use similar food-finding techniques. This design minimizes the potential irrelevance of heterospecific demonstrations when observers and tutors use different, species-typical foraging behaviours in the field; the irrelevance could lead to a false positive result (type 1 error) should observers learn more poorly from a heterospecific due to this difference only (Klopfer, 1961). The problem could theoretically apply to grackles and doves, since the former often use open beak probing and pulling movements when searching for food, while the latter primarily show closed beak pecking.

Methods

The subjects were 27 adult Carib grackles and 2 Zenaida doves. Twenty-five grackles served as observers in the experiment, while the 2 remaining grackles and the 2 Zenaida doves were trained as tutors. All birds were caught in baited drop traps on the grounds of the Bellairs Research Institute of McGill University, St-James, Barbados. In the coastal area around Bellairs, small mobile flocks of grackles routinely forage in unaggressive, mixed species aggregations with territorial Zenaida doves (see Dolman *et al.*, 1996, for a description of dove-grackle foraging interactions in the field); the two species can be caught simultaneously in traps baited with cooked rice. Upon capture, all birds were weighed, fitted with coloured leg-bands, transferred to individual, wire mesh cages and given food and water *ad libitum* for a minimum of 3 days. Holes were cut on two sides of the wire mesh cages to allow the birds to feed and drink from dishes placed outside; in the demonstration and testing phases of the experiment, the holes also gave access to the learning apparatus. Food for the doves included a commercial seed mix, bread and cooked rice; animal protein (chicken, cheese) was added to the grackle diet. Housing and experiments were conducted in separate, visually-isolated sections of a large outdoor aviary situated on the grounds of the Bellairs Research Institute.

In the tutor training phase, the 2 Carib grackles and the 2 Zenaida doves were shaped to remove the stopper on an opaque, inverted test tube containing hidden seed (Fig. 1A; see also Giraldeau & Lefebvre, 1987). Visible food (cooked white rice) was first placed on the

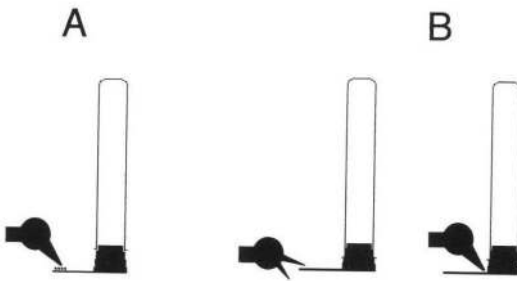


Fig. 1. Apparatus used for training, tutoring and testing. A: Tutor shaping for experiment 1. B: opening techniques that grackle (left) and Zenaida dove (right) tutors were shaped to use in experiment 2; the figure also illustrates the criteria used for analyzing observer responses (left: open beak technique; right: closed beak technique).

stick glued to the stopper; the latter was very loosely pushed into place in a way that made it fall at the slightest contact, revealing the food hidden inside (cooked rice, slightly dried to prevent it from sticking). All 4 tutors were shaped to perform similar pecking movements at the stick, in the absence of any visible food and with the stopper pushed sufficiently tight into the tube to require a persistent and (to an observing bird) obvious series of downward pecks to open it. Tutors were over-trained so that their mean latency to opening was less than 5 s (see below).

The 25 naive grackles were randomly assigned to one of 3 groups: untutored (UT, $N = 5$), grackle-tutored (GT, $N = 10$) and dove-tutored (DT, $N = 10$). Untutored birds were presented with the closed tube containing hidden food, but were neither shaped nor primed like the tutors, nor given opening demonstrations like groups GT and DT. Group UT served as a control for spontaneous ability to solve the task without a demonstration. After being food-deprived for 16-20 hours since 18:00 the preceding evening (just prior to sunset), the 5 UT birds were given 15 trials (5 per day for 3 consecutive days) with a tube presented 3 cm in front of their housing cage. Each of the 15 trials lasted 60 s, with a 90 s inter-trial interval during which the tube was removed from in front of the bird.

For the demonstration and testing phase of groups GT and DT, 1 grackle and 1 Zenaida dove tutors were placed side by side in front of a naive observer grackle. Like the UT subjects, all three birds were in their individual housing cage, a procedure that minimized handling stress. The three cages were 54 cm apart, with tutor cages placed at a 30° angle with respect to the observer to insure visibility of the opening technique. All birds were food-deprived as of 18:00 the previous evening, but had water available to them *ad libitum* before and during trials. Observers were given a total of 20 trials (5 per day for 4 consecutive days). Each trial consisted of a demonstration phase, in which one of the tutors had access to a tube, but the observer did not, and a testing phase, in which the observer had a closed, food-filled tube in front of it, but the tutors did not. On average, the demonstration phase lasted less than 5 s: grackle tutor #1 was used with 5 observers and had a mean latency to opening of 4.30 s ($SD = 1.45$); grackle tutor #2 also demonstrated to 5 subjects with a mean latency of 3.95 s ($SD = 1.50$); dove tutor #1 was used with 6 observers and opened in 4.42 s ($SD = 1.47$), while dove tutor #2 faced 4 observers and had a mean latency of 4.62 s ($SD = 1.41$). During each tube opening demonstration, the

other tutor had an open petri dish placed in front of it, from which it could freely eat a few kernels of visible cooked rice. This served as a control for preferential attention to a particular tutor type, one of which performed a novel technique that would be required in the observer testing phase; the other, a known feeding behaviour that was irrelevant to observer testing (Dolman *et al.*, 1996). Tutor species and left-right position of the tube and petri dish were counter-balanced for all observers. Ten grackles (group DT) saw a dove open a tube and a grackle feed from an open dish. Ten (group GT) grackles saw a pre-trained grackle open its tube and a dove eat from the dish. Five naive birds per group saw the tube-opening tutor on their left; the other 5, on their right.

Following each demonstration, the observer was presented with a closed, food-filled test tube and an empty, open petri dish side-by-side, 3 cm outside its cage; the left-right position of the tube and dish were counter-balanced for all observers. The observer had 30 s in which to open its tube; if it did not open, the tube was removed. There was an inter-trial interval of 90 s before the next demonstration/testing trial given, up to a maximum of 5 trials per day. Five to 10 s separated the demonstration and testing phases of each trial. All trials were conducted between 10:00 and 15:00; both tutors and observers were fed *ad libitum* at the end of a testing day. At the end of the experiment, all birds were fed *ad libitum* and released at their point of capture.

Variables noted by the experimenter (who stood 1.5 m to the side and behind the observer, outside the testing section of the aviary, looking in through a 50 × 30 cm window) were number of trials until first beak contact with the stopper (stick and cork) and number of trials until first successful opening. Tutor species effects on these two dependent variables were tested at the univariate and multivariate level with a MANOVA, since the dependent variables are correlated, but assess distinct effects of tutoring on the actions of observers.

Results

None of the 5 control birds spontaneously opened the apparatus during their 15 trials; one pecked at the stopper once on trial 15. In contrast, 19 of 20 tutored grackles had opened their tube by trial 15; the 20th did so on trial 16. This difference in the number of tutored vs untutored birds who pecked at and opened their tube is highly significant in both cases (Fisher exact $p = 0.002$ for pecking and < 0.001 for opening; Fig. 2A). Unlike the Zenaida doves studied by Dolman *et al.* (1996), none of the grackles touched the empty control dish.

All 10 observers learned in each of tutored conditions. Grackle tutored and dove-tutored subjects showed very similar latencies to first peck and first opening (Fig. 2B; respectively 6.1 trials (SE = 1.04) and 7.4 trials (SE = 0.92) for grackle-tutored birds and 7.5 trials (SE = 1.13) and 8.8 trials (SE = 1.02) for dove-tutored ones). Differences between the tutored groups on the two dependent variables yielded low, non-significant F values both at the multivariate ($F_{2,17} = 0.47$, $p = 0.63$) and univariate

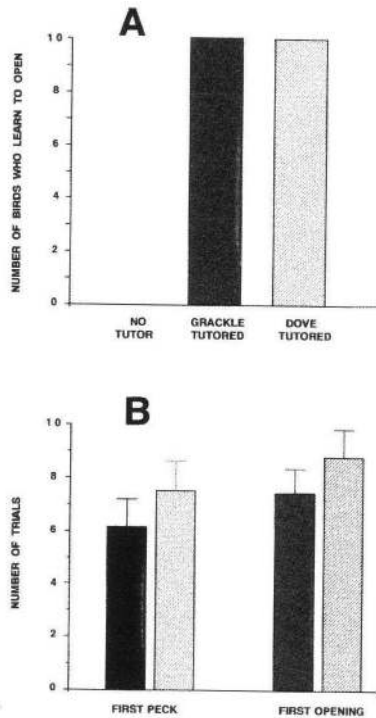


Fig. 2. A: number of birds who learn to open respectively in the untutored, grackle-tutored and dove-tutored conditions of experiment 1. B: mean number of trials to first peck and first opening for observers in the grackle-tutored (black histograms) and dove-tutored (striped histograms) conditions; error bars represent standard errors of the mean.

level (first peck: $F_{1,18} = 0.83$, $p = 0.37$; first opening: $F_{1,18} = 0.99$, $p = 0.33$).

Experiment 2: Different tutor techniques

In this experiment, we trained grackle and Zenaida tutors to use different techniques to remove the stopper from the tube. We did this for two reasons: we first wanted to eliminate the possibility that the results of experiment 1 were due to our tutors using similar opening techniques, thus causing a false negative result (type 2 error). We also wanted to test for motor act imitation using the dual action procedure (Heyes, 1996; Whiten & Custance, 1996; Zentall, 1996) and thus needed two tutor types that demonstrated different motor acts. In training our grackles and Zenaida dove

tutors, we therefore let each one use its normal, species-typical movements (open beak pulling, probing or prying for grackles, closed beak pecking for doves), and then shaped the tutors to accentuate the differences between these techniques.

Methods

Thirty-seven adult Carib grackles and 2 adult Zenaida doves, different from the ones used in experiment 1, were caught in baited drop traps on the grounds of the Bellairs Research Institute of McGill University, St-James, Barbados. The 2 Zenaida doves and 2 of the 37 grackles were trained as tutors for the experiment; the remaining 35 grackles were randomly assigned to one of 3 groups: untutored (UT, $N = 5$), grackle-tutored (GT, $N = 15$) and dove-tutored (DT, $N = 15$). Tutors were housed in individual wire mesh cages throughout the training and demonstration phases; prior to being used in the experiment, however, observer grackles were housed together in an aviary and subsequently transferred to the individual cage in which they remained throughout the demonstration and testing phases. Upon capture, all birds were weighed, fitted with coloured leg bands for identification and given food and water *ad libitum* for 3 days. For grackles, the captive diet involved cooked white rice and commercial mynah pellets; the pellets also served as food reward during the training and experimental phases. Doves were given a commercial seed mix and brown lentils; the lentils, which were visually very similar to mynah pellets, were used as the food reward for doves during training and demonstrations. During the experiment, all food was removed from a subject's cage at 18:00 the evening before a set of trials.

As in experiment 1, the 4 tutors were trained through shaping to remove the stopper on an opaque inverted test tube containing hidden food. Grackle tutors were shown by a human experimenter that the stopper on the tube could be removed by holding the tip of the stick, moving it on a vertical axis and pulling the stopper free; when given their own tube, both grackles removed the stopper with this technique (Fig. 1B). The two Zenaida dove tutors were not shown the pulling technique, but were presented instead, as in experiment 1, with visible food (millet seed) placed near the junction of the stick and cork on a very loosely-fitted stopper; the slightest peck at the seed caused the stopper to fall, shaping the birds to use this technique in further training trials where visible food was progressively removed and the stopper pushed more tightly in the tube (Fig. 1B). As in experiment 1, the 4 tutors were over-trained until their mean latency to opening was below 10 s. Like the observers, tutors had their food removed at 18:00 on the evening preceding a set of trials; on days where the experiment was not being conducted, active tutors were given *ad libitum* access to food. The two back-up tutors were given *ad libitum* access to food every day.

The demonstration and testing phases were similar to those of experiment 1, except that 1) observers were given 60 s instead of 30 s to open their tube on each testing trial; 2) the food available to the grackle tutors and observers was mynah pellets (6 pellets in the case of observers and 3 in the case of tutors, whether hidden in the tube or visible in the control petri dish), and 3) left-right position of the closed tube and empty petri dish given to the observer was systematically opposite to what it had witnessed during each preceding demonstration (all tutor variables were counter-balanced).

All trials were videotaped; the recording system was placed on a tripod 2 m away from the observer grackle. Tapes were later analyzed by two experimenters to determine location

and technique of beak contacts used by the subjects in interacting with the apparatus. Location was either the tip or mid-part of the stick, and the area near the base of the cork, with the stick divided into three equal parts. Two techniques were distinguished: closed beak and open beak. The closed beak technique involved pecking at the stick or cork; the open beak technique included pulling (open beak approach followed by beak closure on the stick), probing (open beak approach followed by the lower mandible pressing down on the stick as the beak continued to open) and prying (beak open, upper mandible pushing against base of tube, lower mandible pushing against stick). As in experiment 1, trial to first beak contact with the stick or cork and trial to first opening were also noted and analyzed both at the univariate and multivariate level with a MANOVA. Tutored subjects who failed to open were assigned the theoretical ceiling value for latency, 21 trials; as a precautionary step, a second MANOVA was conducted by excluding all birds who failed.

Results

As in experiment 1, untutored grackles did not spontaneously search for food in the apparatus: none of the 5 control birds pecked at or opened their tube, while one of them pecked once at its empty control dish on trial 16. In contrast, 20 of the 30 tutored subjects pecked at their tube and 16 successfully opened it. The difference in the number of tutored *vs* untutored birds who pecked at and opened their tube is significant in both cases (Fisher exact $p = 0.009$ for pecking and 0.049 for opening; Fig. 3A). Compared to experiment 1, disturbance from rain, visitors to Bellairs and noise from an adjacent park may have led to the lower proportion of tutored birds who opened in the present experiment.

In the tutored groups, 10 subjects in each condition pecked at their apparatus; 9 grackles in group GT successfully opened it, while 7 birds did in group DT. These frequencies do not differ significantly either for pecking (Fisher exact $p = 1.00$) or opening (Fisher exact $p = 0.72$). Trial to first peck and trial to first opening also do not differ between condition GT and DT (Fig. 3B; trial to first peck: univariate $F_{1,28} = 0.34$, $p = 0.57$; trial to first opening: univariate $F_{1,28} = 0.83$, $p = 0.37$; multivariate test on both dependent variables: $F_{2,27} = 0.47$, $p = 0.62$). The same conclusions apply if we restrict the MANOVA to the 20 subjects who attempted to solve the task (trial to first peck: univariate $F_{1,18} = 0.74$, $p = 0.40$; trial to first opening: univariate $F_{1,18} = 1.33$, $p = 0.26$; multivariate test on both dependent variables: $F_{2,17} = 0.63$, $p = 0.54$). None of the tutored subjects touched the empty control dish.

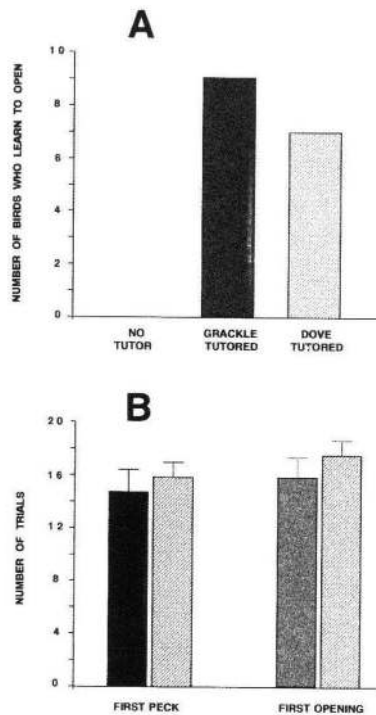


Fig. 3. A: number of birds who learn to open respectively in the untutored, grackle-tutored and dove-tutored conditions of experiment 2. B: mean number of trials to first peck and first opening for observers in the grackle-tutored (black histograms) and dove-tutored (striped histograms) conditions; error bars represent standard errors of the mean.

Dove-tutored and grackle-tutored birds differed in the technique they used to interact with the apparatus. On their first peck at the apparatus, an open beak technique was used by 6 out of 10 grackle-tutored subjects, but by only 1 of the dove-tutored ones; conversely, 9 dove-tutored birds used the closed beak technique, while 4 grackle-tutored subjects did (Fisher exact $p = 0.05$; Fig. 4A). Overall, a mean of 2.2 open beak contacts were made at the tube by grackle-tutored birds, while dove-tutored ones made 0.6; a mean of 5.5 closed beak pecks were made by dove-tutored subjects, while grackle-tutored ones made 2.8 (Fig. 4B). This difference in mean contacts of each type as a function of tutor species is significant at the 0.01 level in the MANOVA ($F_{2,17} = 5.43$, $p < 0.01$; N for this analysis restricted, by definition, to the 20 subjects who attempted to solve the task); it reaches the 0.05 level of significance on the univariate test for closed beak contacts

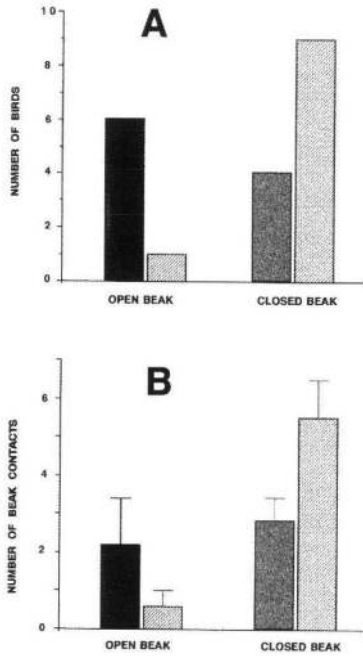


Fig. 4. A: number of grackle-tutored (black histograms) and dove-tutored (striped histograms) birds who used an open beak or a closed beak on their first contact with the stopper. B: mean number of open beak and closed beak contacts made by grackle-tutored (black histograms) and dove-tutored (striped histograms) birds; error bars represent the standard error of the mean.

($F_{1,18} = 4.41$, $p < 0.05$), but fails to reach significance for the univariate test on open beak ones ($F_{1,18} = 2.22$, $p = 0.15$).

Differences between GT and DT observers were restricted to the open vs closed beak techniques and did not include the section of the apparatus contacted by the tutor. All 10 birds who pecked in each group touched the tip of the stick protruding from the stopper, but very few observers touched either the cork or the mid-part of the stick. The mean number of contacts with each section of the apparatus showed no effect of tutor type (multivariate on the 3 parts: $F_{3,16} = 0.90$, $p = 0.46$; univariate tests on, respectively, tip: $F_{1,18} = 0.25$, $p = 0.62$; mid-part: $F_{1,18} = 2.25$, $p = 0.15$; cork: $F_{1,18} = 1.00$, $p = 0.33$).

Discussion

The results of our two experiments suggest that social learning in Carib grackles follows the same ecological rules as those found previously for three populations of Zenaida doves (Dolman *et al.*, 1996; Carlier & Lefebvre, in press) in which social learning was shown to co-vary with differing patterns of scramble competition. Consistent with those findings, Carib grackles, which scramble compete with both grackles and Zenaida doves in Barbados, learned just as readily from a Zenaida dove as they did from a grackle tutor. In addition, the open versus closed beak data from experiment 2 reflect the extractive foraging behavior of Carib grackles: observers imitated the motor variant used by their tutor, whether the tutor was a conspecific or an ecologically relevant heterospecific. Interestingly, observers did not copy the location that tutors had been shaped to interact with (the tip of the stick for the pulling grackle, the vicinity of the cork for the pecking dove). Instead, all observers manipulated the tip of the stick. Thus, the grackles in our study copied the motor act, but did not use the local cues associated with the technique they witnessed. In view of the frequent controversies concerning stimulus and response components of social learning (*e.g.* Visalberghi & Frigaszy, 1990; Whiten, 1993; Byrne & Tomasello, 1995), this is a surprising and noteworthy result.

Over a decade ago, Mason *et al.* (1984) found that red-winged blackbirds (*Agelaius phoeniceus*) learned as readily from a heterospecific scramble competitor, the common grackle (*Quiscalus quisqualis*) as they did from a conspecific. At the time, Mason *et al.* (1984) viewed their finding as counter-intuitive, given their expectation that conspecifics would be the most probable source of social information in the field for a gregarious bird like *A. phoeniceus*. Indeed, Klopfer (1961) had predicted that learning from a heterospecific should be more difficult than learning from a conspecific, a prediction that has since dominated the literature. According to this logic, conspecifics should be more relevant demonstrators of novel foraging techniques because their diet, the morphology of their food-searching structures (beak, head and feet, in the case of Icterids) and the pre-programmed components of their foraging behaviour should be similar.

Our focus on scramble competition suggests an alternative view that incorporates the present results, those of Mason *et al.* (1984), as well as those obtained previously with Zenaida doves. In this view, animals

learn from the feeding competitors they must outperform during scramble competition. When scrambling for food, speed is a major determinant of feeding success; attacks and chases are not used, contrary to the interference competition that characterizes many feeding interactions (Grant, 1993). When scrambling, feeding rate will be affected by the information animals have about the type of food available, its location, and the searching and handling techniques required to obtain it. Both stimulus and response (imitation) forms of social learning are helpful in acquiring this information, and imitation will be all the more important when searching and handling techniques are complex. Both Parker (1996) in her theoretical account and Whiten *et al.* (1996), in their experimental use of artificial 'fruit' requiring intricate extractive manipulations, emphasize this point.

In comparative work, it is important to identify simultaneously those species which exhibit a given behavioral trait (such as imitation) and those which either do not exhibit the trait or exhibit it to a lesser extent. Variables that discriminate between these outcomes are good candidates for evolutionary hypotheses based on ecological pressures (Kamil, 1988). Although imitation has been shown in a variety of unrelated taxonomic groups, in primates (the taxonomic group in which the most species have been tested), the major variable affecting imitation appears to be phyletic. Old and New World monkeys do not show imitation, whereas great apes do (Visalberghi & Fragaszy, 1990; Whiten & Ham, 1992). Whether this difference is an effect of encephalization and cognition (Russon *et al.*, in press) or a result of dietary specialization on embedded foods (Parker, 1996), however, is difficult to determine. In this case, more comparative work based on ecological variables is clearly needed (Heyes, 1993).

If, as our results suggest, both scramble competition and complexity of food handling techniques do indeed favor imitation (Russon *et al.*, in press), the strongest ecological test would make opposite predictions for stimulus and response forms of social learning based on foraging ecology. For example, all other things being equal, taxon A, if it uses more complex food handling techniques than taxon B, should imitate more readily than taxon B. To control for confounding variables, however, one would also predict that taxon B, if it uses scramble competition to a greater extent than taxon A, would acquire stimulus forms of social learning more readily than taxon A. In view of the methodological problems that often face the comparative

study of learning (McPhail, 1982; Lefebvre, 1996; Lefebvre & Giraldeau, 1996), such opposite predictions could help bring the study of imitation towards the rigour and strong inference techniques that characterize other fields of comparative biology (Harvey & Pagel, 1991).

References

- Akins, C.K. & Zentall, T.R. (1996). Imitative learning in male Japanese quail (*Coturnix japonica*) using the two-action procedure. — *J. Comp. Psychol.* 110, p. 316-320.
- Bonner, J.T. (1980). *The evolution of culture in animals*. — Princeton University Press, Princeton.
- Byrne, R.W. & Tomasello, M. (1995). Do rats ape? — *Anim. Behav.* 50, p. 1417-1420.
- Carlier, P. & Lefebvre, L. (1996). Differences in individual learning between group-foraging and territorial Zenaida doves. — *Behaviour* 133, p. 1197-1207.
- — & — — (in press). Ecological differences in social learning between adjacent, mixing populations of Zenaida doves. — *Ethology*.
- Dawson, B.V. & Foss, B.M. (1965). Observational learning in budgerigars. — *Anim. Behav.* 13, p. 470-474.
- Dolman, C., Templeton, J.T. & Lefebvre, L. (1996). Mode of foraging is related to tutor preference in *Zenaida aurita*. — *J. Comp. Psychol.* 110, p. 45-54.
- Ffrench, R. (1973). *A guide to the birds of Trinidad and Tobago*. — Macmillan, London.
- Galef, B.G., Jr (1988). Imitation in animals: history, definition, and interpretation of data from the psychological laboratory. — In: *Social learning: Psychological and biological perspectives* (T.R. Zentall & B.G. Galef, Jr, eds). Lawrence Erlbaum, Hillsdale, p. 3-28.
- —, Manzig, L.A. & Field, R.M. (1986). Imitation learning in budgerigars: Dawson & Foss (1965) revisited. — *Behav. Proc.* 13, p. 191-202.
- Giraldeau, L.-A. & Lefebvre, L. (1987). Scrounging prevents cultural transmission of food-finding behaviour in pigeons. — *Anim. Behav.* 35, p. 387-394.
- Grant, J.W.A. (1993). Whether or not to defend? The influence of resource distribution. — *Mar. Behav. Physiol.* 23, p. 137-153.
- Harvey, P.H. & Pagel, M.D. (1991). *The comparative method in evolutionary biology*. — Oxford University Press, Oxford.
- Heyes, C.M. (1993). Imitation, culture and cognition. — *Anim. Behav.* 46, p. 999-1010.
- — (1996). Genuine imitation? — In: *Social learning in animals: The roots of culture* (C.M. Heyes & B.G. Galef, Jr, eds). Academic Press, New York, p. 371-390.
- —, Dawson, G.R. & Nokes, T. (1992). Imitation in rats: initial responding and transfer evidence. — *Quart. J. exp. Psychol.* 45B, p. 81-92.
- Kamil, A.C. (1988). A synthetic approach to the study of animal intelligence. — In: *Comparative perspectives in modern psychology*. Nebraska Symposium on Motivation, Vol. 35 (D.W. Leger, ed.). University of Nebraska Press, Lincoln, p. 257-308.
- Kawai, M. (1965). Newly acquired pre-cultural behavior of a natural troop of Japanese monkeys on Koshima island. — *Primates* 6, p. 1-30.
- Klopfer, P.H. (1961). Observational learning in birds: the establishment of behavioural modes. — *Behaviour* 17, p. 71-80.

- Lefebvre, L. (1996). Ecological correlates of social learning: problems and solutions for the comparative method. — *Behav. Proc.* 35, p. 163-171.
- — & Giraldeau, L.A. (1996). Is social learning an adaptive specialization? — In: *Social learning in animals: The roots of culture* (C.M. Heyes & B.G. Galef, Jr, eds). Academic Press, New York, p. 107-128.
- McPhail, E.M. (1982). *Brain and intelligence in vertebrates*. — Clarendon Press, Oxford.
- Mason, J.R., Arzt, A.H. & Reidinger, R.F. (1984). Comparative assessment of food preferences and aversions acquired by blackbirds via observational learning. — *Auk* 101, p. 796-803.
- Palameta, B. (1989). The importance of socially-transmitted information in the acquisition of novel foraging skills by pigeons and canaries. — PhD thesis, King's College, Cambridge University, UK.
- — & Lefebvre, L. (1985). The social transmission of a food-finding technique: what is learned? — *Anim. Behav.* 33, p. 892-896.
- Parker, S.T. (1996). Apprenticeship in tool-mediated extractive foraging: Imitation, teaching and self-awareness in great apes. — In: *Reaching into thought: The minds of the great apes* (A.E. Russon, K.A. Bard & S.T. Parker, eds). Cambridge University Press, Cambridge, p. 348-370.
- Russon, A.E., Mitchell, R.W., Lefebvre, L. & Abravanel, E. (in press). The comparative evolution of imitation. — In: *Piaget, evolution and intelligence* (J. Langer & M. Killen, eds). Lawrence Erlbaum, Hillsdale.
- Sasvari, L. (1985). Different observational learning capacity in juvenile and adult individuals of congeneric bird species. — *Z. Tierpsych.* 69, p. 293-304.
- Suboski, M.D. (1990). Releaser-induced recognition learning. — *Psychol. Rev.* 97, p. 271-284.
- Thorpe, W.H. (1963). *Learning and instinct in animals*. — Methuen, London.
- Visalberghi, E. & Fragaszy, D.M. (1990). Do monkeys ape? — In: *Language and intelligence in monkeys and apes: Comparative developmental perspectives* (S. Parker & K. Gibson, eds). Cambridge University Press, Cambridge, p. 247-273.
- Voous, K.H. (1983). *Birds of the Netherlands Antilles*. — De Walburg Pers, Utrecht.
- Whiten, A. (1993). Human enculturation, chimpanzee enculturation and the nature of imitation. — *Behav. Brain Sci.* 16, p. 538-539.
- — & Custance, D.M. (1996). Studies of imitation in chimpanzees and children. — In: *Social learning in animals: The roots of culture* (C.M. Heyes & B.G. Galef, Jr, eds). Academic Press, New York, p. 291-318.
- —, Custance, D.M., Gomez, J.-C., Teixidor, P. & Bard, K.A. (1996). Imitative learning of artificial fruit processing in children (*Homo sapiens*) and chimpanzees (*Pan troglodytes*). — *J. Comp. Psychol.* 110, p. 3-14.
- — & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. — *Adv. Stud. Behav.* 21, p. 239-283.
- Zentall, T.R. (1996). An analysis of imitative learning in animals. — In: *Social learning in animals: The roots of culture* (C.M. Heyes & B.G. Galef, Jr, eds). Academic Press, New York, p. 221-244.
- —, Sutton, J. & Shelburne, L.M. (1996). True imitative learning in pigeons. — *Psychol. Sci.* 7, p. 343-346.
-