EFFECTS OF SOCIAL FACILITATION AND OBSERVATIONAL LEARNING ON FEEDING BEHAVIOR OF THE RED-WINGED BLACKBIRD (*AGELAIUS PHOENICEUS*)

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ABSTRACT.—In the presence of food-deprived and therefore rapidly feeding Red-winged Blackbirds (*Agelaius phoeniceus*), pairs of nondeprived conspecifics increased their own food consumption and spillage. The effect of social facilitation appeared amplified when both pairs of birds were food-deprived. Blackbirds also showed clear differential preferences for novel foods based on observations of male conspecifics consuming and spilling novel food. Social facilitation of feeding and observational learning of differential food preferences for novel foods may help to explain the Red-winged Blackbird's tendency to locate and exploit (i.e. damage) crops during short periods when the crops are especially vulnerable. Received 30 January 1981, accepted 21 April 1981.

SOCIALLY facilitated behavior such as flocking may protect birds from predators (Conner et al. 1975, Clayton 1979, Lazarus 1979) and contribute to reproductive synchrony (Roell 1978). Social facilitation may also lead to a more complete exploitation of food resources by birds through more rapid selection of new foods (Davies 1976, Traemer and Kemp 1979) or through increased food consumption (Rubenstein et al. 1977, Feare and Inglis 1979). Consumption is influenced by the feeding rates of neighboring birds in a flock, regardless of their sex, or, sometimes, their species (Fairchild et al. 1977). In addition, consumption is discriminative for most species, i.e. individuals forage selelctively and tend to choose foods that other birds in the flock are choosing (e.g. Murton 1971, Williamson and Grey 1975).

Social facilitation of food selection among members of a flock may have deleterious agricultural consequences. For example, foraging based on observational learning may encourage the selective crop damage that is often produced by gregarious pests, such as Red-winged Blackbirds (*Agelaius phoeniceus*). Here, we report two experiments that demonstrate that: (1) Red-winged Blackbirds will increase their feeding activity in the presence of feeding conspecifics; and (2) Red-winged Blackbirds differentially select some foods as a result of observing the behaviors of other individuals.

EXPERIMENT 1, SOCIAL FACILITATION OF FEEDING

METHODS

Subjects.—Forty adult male Red-winged Blackbirds were wild-trapped during October 1980 at the U.S. Fish and Wildlife Ohio Field station and acclimated to captivity for 7 weeks before the experiment. The birds were housed in pairs in large (36 cm long × 61 cm wide × 41 cm high) cages in a room with an ambient temperature of about 23°C. A 6 h/18 h light/dark cycle was used to maximize the feeding rates of the birds without reducing the total quantity of food consumed (Rogers 1974). Water was always available, and, before the experiment began, the birds were permitted to feed *ad libidum* on Purina Flight Bird Conditioner (PFBC) and apples.

Procedure.—The 20 pairs of birds were assigned to 10 groups (2 pairs per group). The two cages holding the pairs of birds in each group were placed adjacent to and in view of one another in a cage rack. Each group was visually isolated from the others with pieces of cardboard (36 cm long × 61 cm wide). All pairs of birds were given free access to PFBC, and consumption and spillage were measured

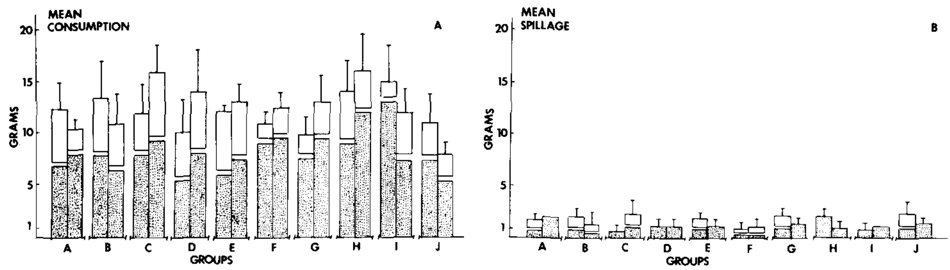

Fig. 1. Mean consumption (A) and spillage (B) of Purina Flight Bird Conditioner (PFBC) by each group of blackbirds over the 6-h light period on the 4 days before experimental treatments. The stippled areas indicate the mean consumption of PFBC by each group during the 1st h after light onset. Vertical bars represent standard errors of the mean.

1, 2, and 6 h after the onset of light for 4 consecutive days. Food was presented from two cups (about 5 cm apart) located at the front of the cage (Rogers 1974). Each cup (7.5-cm diameter) was placed within a larger cup (11.3-cm diameter) that caught spillage from the smaller one during feeding. Consumption and spillage were measured, because both might be considered aspects of bird exploitation (i.e. damage) of crops. For example, birds can produce primary damage by consuming sunflower seeds or secondary damage by removing, but not consuming, seeds from the heads of the sunflower. The latter sort of damage might be considered analogous to food that the birds spill but do not eat.

During the dark period of the fourth day, the first of two experimental treatments was given. In six groups (C–H), one pair of birds (but not the other) was food-deprived. Food deprivation consisted of removing PFBC (but not apples) from the birds' cages for the 18 h of darkness. In two other groups (I, J), both pairs were food-deprived. In the remaining two groups (A, B), both pairs received food. Consumption and spillage of PFBC by each pair of birds was measured during the 1st, 2nd, and 6th h after the onset of light on the day immediately following the experimental treatment. Then, during the subsequent dark cycle, a second experimental treatment was given in which the feeding schedules were reversed: previously nondeprived birds were deprived, while previously deprived birds were not. Consumption and spillage of PFBC were measured as before on the day immediately following the second experimental treatment.

Analysis.—Measurements of consumption (for each pair of birds) were assessed using analysis of variance (ANOVA). A one-way ANOVA with repeated measures on hour (1st, 2nd, 6th) of measurement was used to test for differences between groups before the experimental treatments. Three-way ANOVAs with repeated measures on two factors (treatment condition, hour of measurement) were used to assess consumption and spillage after experimental treatments. In separate ANOVAs, the following comparisons were made: mean pretreatment consumption versus consumption after the first experimental treatment; mean pretreatment consumption versus consumption after the second experimental treatment; and consumption after the first versus the second experimental treatment. Spillage data were assessed in the same way. Tukey *a* tests ($P < 0.05$; Winer 1962) were used to isolate significant differences among means.

Results

During the 4 days before the first experimental treatment, there were no significant differences ($P > 0.25$) among any of the pairs of birds for either consumption (Fig. 1A) or spillage (Fig. 1B). When compared with pretreatment levels, however, the first experimental treatment affected both consumption [$F(1, 16) = 10.04$, $P < 0.05$] and spillage [$F(1, 16) = 52.3$, $P < 0.05$]. For groups C–H, both the deprived and nondeprived birds consumed and spilled significantly more PFBC during the 1st (Fig. 2A, 2B) and 2nd h of the light cycle, but not by the 6th h ($P > 0.25$). For groups I and J, all pairs of birds (all food-deprived) consumed and spilled significantly more PFBC during all hours of measurement. Pairs in groups I and J also

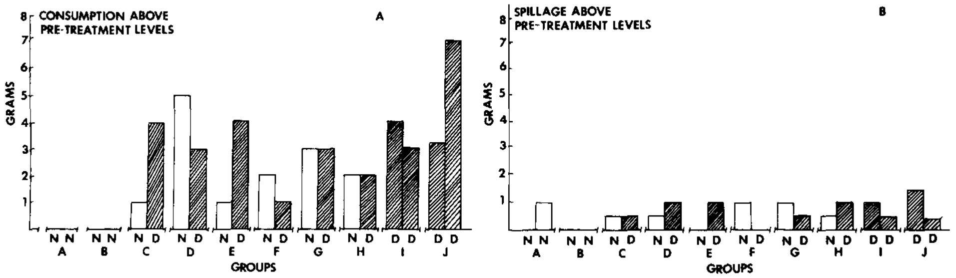

Fig. 2. The consumption (A) and spillage (B) of PFBC that exceeded pretreatment levels for each group after the first experimental treatment.

consumed and spilled significantly more food during all hours than did the birds in groups C–H. For groups A and B, none of the pairs of birds (none food-deprived) consumed or spilled more food than before the experimental treatment ($P > 0.25$).

When compared with the pretreatment levels, the second treatment also affected consumption [$F(1, 16) = 27.7$, $P < 0.05$] and spillage [$F(1, 16) = 106.0$, $P < 0.05$]. The pattern of differences after the second experimental treatment was similar to that following the first experimental treatment. For groups C–H, both deprived and nondeprived birds again consumed and spilled significantly more PFBC during the 1st (Fig. 3A, 3B) and 2nd h of the light cycle, but not by the 6th h ($P > 0.25$). For groups I and J (none food-deprived), consumption and spillage were similar to the pretreatment levels ($P > 0.25$). For groups A and B (all food-deprived), consumption and spillage of PFBC increased significantly over pretreatment levels. Unlike the first treatment, however, consumption and spillage for the groups (A, B) in which both pairs of birds were food-deprived were not significantly greater ($P > 0.25$) than for groups C–H, in which only one of the pairs was food deprived.

Finally, when compared with the effects of the first treatment, effects of the second treatment on consumption and spillage differed significantly [$F(1, 16) = 5.2$, $P < 0.05$; $F(1, 16) = 7.6$, $P < 0.05$, respectively]. Pairs of birds in both groups I and J consumed and spilled significantly less PFBC when they were not food-deprived (second experimental treatment) than when they were food-deprived (first experimental treatment). Likewise, birds in groups A and B consumed and spilled less PFBC when they were not food-deprived (first treatment) than when they were food-deprived (second treatment).

DISCUSSION

From the results of Experiment 1, we concluded that social facilitation can influence consumption and spillage of a familiar food (i.e. PFBC) by adult male Red-winged Blackbirds. Nondeprived birds increased their consumption and spillage when exposed to food-deprived feeding conspecifics (groups C–H) and the effect was amplified in one test when both pairs of birds were food-deprived (groups I and J after the first experimental treatment). Such behavior could account for much of the damage attributed to these birds, because informal observations suggest that individual Red-wings damage more of a crop when feeding together in flocks than when feeding alone (Dolbeer, pers. comm.). That speculation is consistent with observations that other birds eat more when together in flocks than when solitary (Caraco

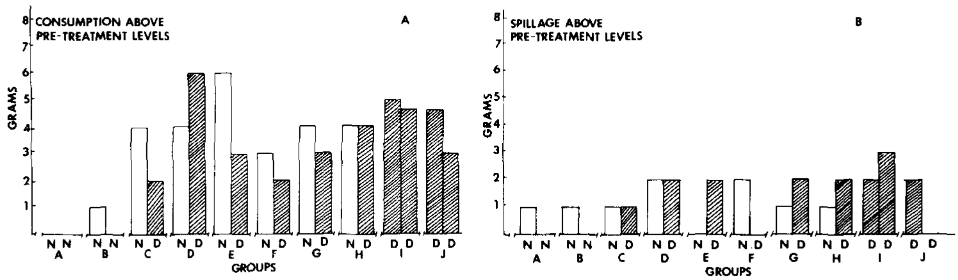

Fig. 3. The consumption (A) and spillage (B) of PFBC that exceeded pretreatment levels for each group after the second experimental treatment.

et al. 1980, Baker et al. 1981) and locate food sources by joining others seen to be feeding (Klopfer 1959, Crook 1960, Ward 1965, Murton 1974).

Experiment 2, Discriminative Feeding Based on Observational Learning

An important question, not addressed by Experiment 1, is whether Red-winged Blackbirds select some foods rather than others as a result of observational learning. Observational learning [defined by Wilson (1975) as unrewarded learning that occurs when one organism watches the activities of another] by blackbirds could result in damage that is concentrated on particular crops or fields. More important, such crops need not be those with which depredating flocks have had extensive experience. Observational learning could override the birds' usual avoidance responses (i.e. neophobia) to unfamiliar foods. Experiment 2 was designed to assess whether adult male Red-winged Blackbirds would eat a novel food having seen other conspecifics feeding on that food.

Methods

Subjects.—The 40 adult male Red-winged Blackbirds used in Experiment 1 were housed under the same conditions for Experiment 2.

Stimuli.—The food types used in Experiment 2 were green or orange pastries (about 0.25-cm diameter) made from flour, water and food coloring (Durkee Food Colors). The pastries were colored orange or

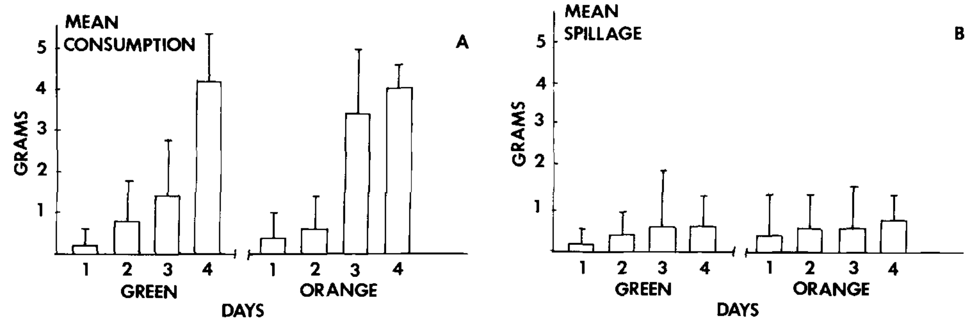

Fig. 4. Mean consumption (A) and spillage (B) of green or orange pastry during training. Consumption of both pastry types increased over days, so that by the 4th day, 87% of the green pastry and 82% of the orange pastry presented was consumed. Vertical bars represent standard errors of the mean.

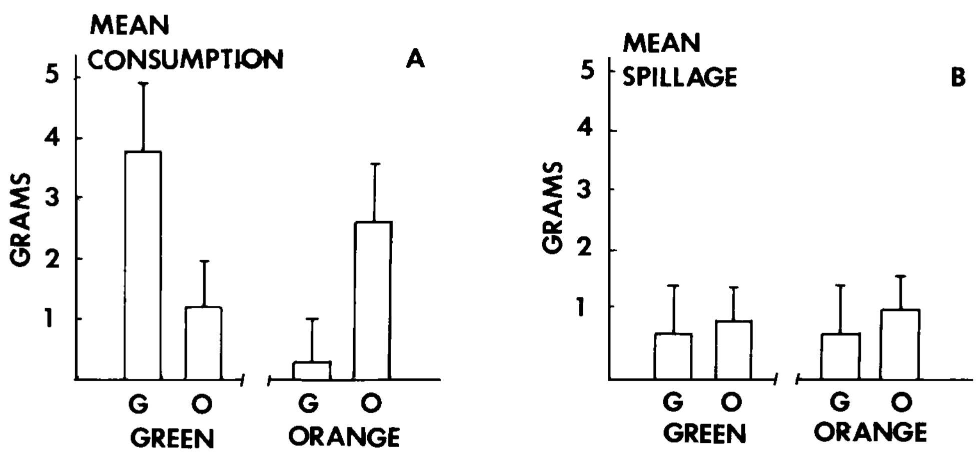

Fig. 5. Mean consumption (A) and spillage (B) of green or orange pastry by green-trained or orange-trained observer birds during preference tests. Vertical bars represent standard errors of the mean.

green because these colors have been used frequently in other investigations of foraging by granivorous birds (e.g. Brower 1960, Reiskind 1965).

Procedure.—The 20 pairs of birds were randomly assigned to 10 groups, and the cages holding the pairs of birds in each group were placed adjacent to and in view of one another in cage racks. Each group was visually isolated from the others as before. Training was then given for 4 days. For five of the groups, one pair of birds was food-deprived for the first 2 h of light on each of the 4 days and then given 5 g of green pastry to consume over the remaining 4 h of light. For the other five groups, one pair was food-deprived for the first 2 h of the light cycle on each of the 4 days and then given 5 g of orange pastry. The other pairs in each group were given PFBC to eat *ad libidum*. All birds were given PFBC *ad libidum* during the dark period of each training day. On the 5th day, the pairs of birds in each group that had been given only PFBC during training were given preference tests between orange and green pastries, while birds given pastries during training were given PFBC to eat *ad libidum*. The amount of each pastry consumed or spilled was recorded.

Analysis.—Measurements of consumption (for each pair of birds) were assessed using ANOVA with repeated measures on the second factor (days) to test for the effects of training on consumption of orange- and green-colored pastries. Another two-way ANOVA with repeated measures on the second factor (pastry color) was used to test for differential selection of pastries by untrained Red-wings.

RESULTS

Consumption of green pastry was similar to consumption of orange pastry during training ($P > 0.25$) (Fig. 4A). Patterns of spillage were also similar ($P > 0.25$) (Fig. 4B). Based on combined analyses, however, consumption and spillage of both pastries increased significantly over the 4 training days [$F(2, 24) = 32.4$, $P < 0.05$; $F(3, 24) = 28.7$, $P < 0.05$, respectively]. By the 4th day of training, the mean consumption by birds given green pastry was 4.34 g (87% of the pastry given), while that of birds given orange pastry was 4.10 g (82% of the pastry given).

During the preference tests, birds consumed and spilled significantly more of the pastry that they had observed other birds consume or spill [$F(1, 8) = 15.8$, $P < 0.05$; $F(1, 8) = 14.1$, $P < 0.05$; green and orange observers, respectively]. In every case, the pair of birds exposed to birds eating and spilling orange pastry subsequently ate and spilled more orange than green pastry, and vice versa (Fig. 5A, 5B).

DISCUSSION

Male Red-winged Blackbirds show clear differential preferences between colored pastries based on their previous observations of conspecifics' consumption and spillage. This finding concurs with earlier findings that some other species of birds modify their feeding behaviors to conform with the behaviors of feeding conspecifics (e.g. Duecker 1976).

GENERAL DISCUSSION

Imitative foraging and observational learning of food preferences have been suggested as adaptive behaviors that support flocking in other species. For example, Chaffinches (*Fringilla coelebs*) commence feeding and sample new foods when exposed to other Chaffinches doing so. The behaviors may permit Chaffinches to locate and switch to new feeding sources readily. Likewise, Starlings (*Sturnus vulgaris*) may increase feeding efficiency while minimizing expenditure of energy through social feeding (Hamilton and Gilbert 1969).

Observational learning and social facilitation, as demonstrated in the present experiments, are two behaviors that could partially explain the blackbirds' ability to discover and exploit vulnerable but patchy food resources (Wilson 1975), such as maturing sunflowers.

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