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Food avoidance by adult house finches, *Carpodacus mexicanus*, affects seed preferences of offspring

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Abstract. In altricial birds, the food habits of young birds may be affected by extended parental contact. To examine this, five nesting pairs of captive adult house finches were exposed to hulled oats treated with an aversive agent, methiocarb. During the nestling and early fledgling stages, juvenile finches raised by adults that avoided oats received 30–40 times less exposure to hulled oats than did juveniles raised by adults that ate oats. After they were separated from the adults, the juveniles had no further access to oats or to canary seed, the alternative untreated food, until tested individually at 10–12, 20–22, and 35–38 weeks of age. There was no relationship between the juvenile birds' exposure to oats in the early nestling stage and their subsequent oat preference scores. Birds raised by adults that avoided oats during the late nestling and fledgling stages, however, displayed lower oat preference scores than did birds raised by adults that ate oats. Thus, dietary aversion to oats established in adult birds was expressed in the seed preferences of their offspring.

Experiences in the first weeks of a bird's life influence numerous later behaviour patterns (Immelmann 1972; Skutch 1976; Glück 1984; Baptista & Petrinovich 1986). For many birds, extended parental contact provides opportunities to learn where and what to eat. Although the notion that the food preferences of young altricial birds are greatly influenced by association with their parents is a familiar one (e.g. Kear 1962; Newton 1967; Alcock 1973), it has been subjected to little experimental inquiry. An exception was Rabinowitch (1969) who restricted breeding pairs of zebra finches, *Poephila guttata*, to a single type of seed until the offspring were 4 weeks old and able to feed themselves. He then gave the young birds preference tests involving their rearing seed and two alternatives. The tests were repeated when the birds were 21–22 weeks old. In most cases, birds preferred the seed to which they were exposed early in life.

In this study, my objective was to determine whether food avoidance behaviour by adult house finches was expressed in the food habits of their offspring. In nature, learning what to eat by trial and error might be costly, and both adults and young would benefit by transmission of the experienced birds' knowledge of suitable food to the offspring (Galef 1975).

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METHODS

Bird Care and Maintenance

I trapped five pairs of house finches near Davis, Yolo County, California and put them into separate outdoor breeding cages (2.7 × 1.8 × 2.2 m) equipped with nest boxes and bundles of cut branches. Each cage had a wooden shelf at the front which held food. Cloth screens on the sides and back of the cages prevented visual contact between birds feeding at the shelves. Throughout the study, the birds' maintenance diet was safflower and white millet seeds supplemented with commercial vitamins, apples and leaf lettuce. Mealworms (*Tenebrio* sp.) were added during the breeding season. Grit and water were always available. After the study, I released all birds.

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Training Adult Finches to Avoid Oats

In preliminary feeding trials (Avery, unpublished data), I found that adult house finches generally preferred oats to canary seed. When I determined that a given pair of adult finches was incubating, they began daily 1-h feeding trials. Within 2 h of sunrise and following a 1-h deprivation period, I placed 5 g of canary seed and 5 g of hulled oats in clear glass bowls at opposite ends of the food shelf. During the training period, the hulled oats were treated with 0.2% (g/g) methiocarb, a chemical used in avian food avoidance learning experiments (e.g. Mason et al. 1984; Avery 1985; Avery & Nelms 1990). After 1 h, the bowls were removed, the contents weighed, and maintenance food provided again. Extensive observations of the birds' feeding behaviour revealed very little spillage, so no correction was necessary. Similarly, mass gained or lost due to ambient humidity was 1% or less and was therefore ignored.

Training lasted until nestlings were present, 6–10 days, depending upon when I discovered that incubation was under way. For pairs with second clutches, the training process was repeated. I anticipated that the training with methiocarb-treated oats would cause some adults to avoid eating oats altogether but would affect others less. Because there was no reinforcement with treated oats after nestlings were present, I expected that avoidance responses would wane over time. The result would be differential exposure of the young birds to oats depending upon the strength of the aversion induced in the adults that raised them.

Exposure of Juvenile Finches to Oats

After eggs hatched, I presented only untreated seed, following the same daily feeding trial procedure described earlier. I divided juvenile–adult association into three 7-day periods: early nestling, late nestling and fledgling. During the early nestling period, all offspring were with their natural parents. In the late nestling period, I cross-fostered nine of the 15 juveniles so that those with adults that avoided oats in the early nestling stage were raised as late nestlings and fledglings by adults that ate oats, and vice versa.

As a relative measure of the juvenile birds' exposure to oats, I used daily oat consumption by birds in each breeding cage during the 1-h feeding trials. I classified juvenile finches as 'not exposed' if oat consumption for a 7-day period was less than 1 g. Total consumption greater than 1 g put the bird in the 'exposed' category for that 7-day period. It was not possible to distinguish food consumed by the adult birds from that fed to the offspring. I used one-way analyses of variance to test for differences in oat consumption between exposed and not exposed groups.

Oat Preferences of Juvenile Finches

When juvenile finches were 5–6 weeks old, I separated them from the adults and moved them to communal holding cages. I tested juveniles for their oat preferences at 10–12 weeks (test 1), 20–22 weeks (test 2) and 35–38 weeks (test 3) of age. During a 3-day acclimation period to the $45 \times 45 \times 45$-cm individual indoor test cages, the birds received the maintenance diet. Then, on the next five mornings, after a 1-h food deprivation period, I offered each bird 5 g of oats and 5 g of canary seed in separate cups. The birds could not see each other during the feeding trials. After 1 h, I weighed the contents of the cups and determined consumption by subtraction. I alternated positions of the seed types daily. After the fifth test day, I returned the birds to their communal outdoor holding cages.

I calculated oat preference scores (oat consumption divided by total consumption) daily for each juvenile finch. A score of 0.5 indicated indifference, and scores greater than or less than 0.5 indicated preference or avoidance of oats, respectively. I used the median of each bird's 5 daily preference scores for statistical analysis with the Kruskall–Wallis test to examine differences in juvenile oat preferences between groups exposed and not exposed to oats.

Because seed selection by house finches may be affected by bill size, for each juvenile bird I measured culmen length, bill depth and bill width to the nearest 0.1 mm with calipers (Pyle et al. 1987). I then computed a correlation coefficient (r) between each of these measurements and the birds' oat preference scores.

RESULTS

The 5 pairs of adult finches produced 15 juveniles used in this study. One juvenile died between the

Table I. Consumption of oats during 7-day early nestling, late nestling, and fledgling periods in cages with juvenile house finches classified as being exposed or not exposed to oats

Stage	Mean (SE) consumption (g)	*N*	$F_{1,13}$	*P*
Early nestling				
Not exposed	0.14 (0.03)	12		
Exposed	5.29 (1.19)	3	95.6	<0.001
Late nestling				
Not exposed	0.11 (0.04)	7		
Exposed	3.41 (1.04)	8	8.6	0.011
Fledgling				
Not exposed	0.09 (0.01)	6		
Exposed	3.35 (0.72)	9	13.4	0.003

second and third oat preference test. Two pairs had two broods and the other pairs had one brood each. Presentation of methiocarb-treated oats to the adult finches resulted in initial avoidance of oats by all but 1 pair. Thus, 12 of the 15 juveniles had little exposure to oats during the early nestling stage (Table I). The relative exposure to oats was more balanced during the late nestling and fledgling stages, because some nestlings were cross-fostered, and because without additional methiocarb treatment, oat consumption by some adults increased over time.

Exposure to oats during the early nestling stage did not affect the preferences expressed by juvenile finches during test 1 ($H=0.33$, $P=0.564$), 2 ($H=1.02$, $P=0.312$) or 3 ($H=0.15$, $P=0.697$). Conversely, young birds not exposed to oats in the late nestling and fledgling stages displayed lower ($P=0.004$–0.029) oat preference scores during each preference test than did those exposed to oats (Fig. 1). There was no correlation ($P>0.05$) between the oat preference scores and culmen length ($r=-0.41$), bill depth ($r=-0.31$) or bill width ($r=0.22$).

DISCUSSION

Nice (1943) suggested that three classes of factors influence food choice in birds: (1) inheritance, (2) trial and error and (3) social learning. If bill size affected seed choice, then larger-billed birds would be expected to prefer oats to canary seed. In this study, selection of oats by juvenile finches was not correlated with bill morphology, which in house finches has a genetic component (Aldrich 1982). Furthermore, exposure to oats during the early nestling stage, when all juvenile finches were with their biological parents, was not related to the subsequently expressed preferences (Fig. 1).

After fledging, each juvenile had ample opportunity to sample the two seed types. Thus, if trial and error learning was the principal determining factor in the juvenile birds' choice of canary seed or oats, then all should have converged on the same preference score, but they did not (Fig. 1).

Social learning through parental contact probably explains the observed difference in oat preference between the restricted and not restricted groups of juveniles. At least three processes could have contributed to this outcome. First, the juveniles may have remembered the taste and/or texture of the seeds fed to them as nestlings and later matched them with the properties of the food they ate themselves. Adult finches feed their young by regurgitation (Thompson 1960), so the transmission of flavour cues in partially digested food is possible. Although food preferences of rat, *Rattus norvegicus*, pups are affected by flavour cues obtained during nursing (Galef & Henderson 1972; Galef & Sherry 1973), the influence of flavour in the diet of nestling birds is unknown. Second, fledglings may have learned what to eat by watching the adults. Food choice in some bird species can be affected by observational learning (e.g. Klopfer 1959; Mason & Reidinger 1982), and such learning may have occurred here also. Third, by actually following the adults to the food bowls, the young birds' initial self-feeding experience probably was the seed type preferred by the adults. In adults that avoided oats, the preferred type was canary seed. Approach and follow

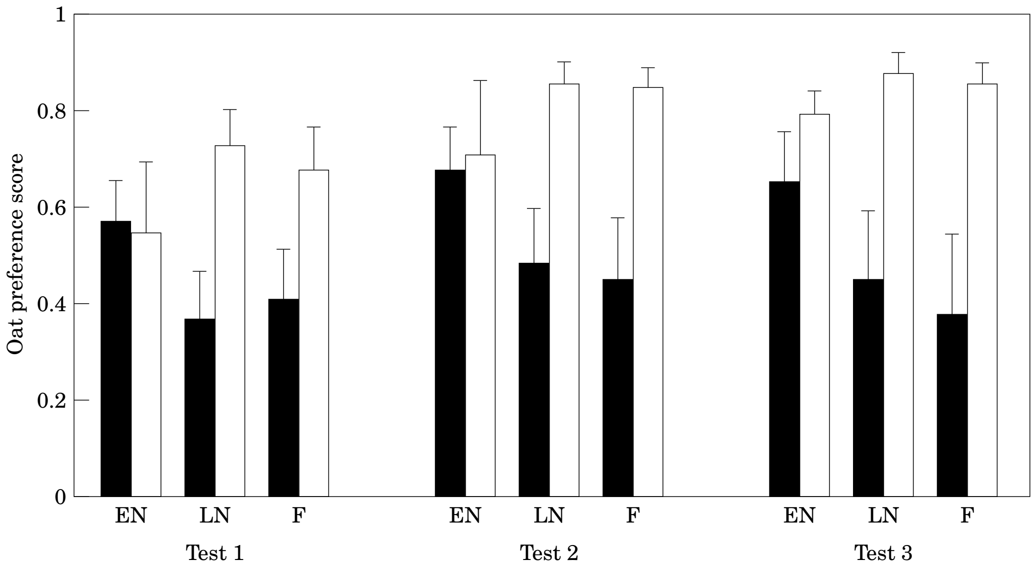

Figure 1. Mean oat preference scores for groups of juvenile house finches not exposed (solid bars) or exposed (open bars) to hulled oats when they were 1–7 (early nestling, EN), 8–14 (late nestling, LN) and 15–21 (fledgling, F) days old. Birds in the not-exposed group were with adults trained to avoid oats, and young birds exposed to oats were with adults that ate oats. Preference scores (oat consumption divided by consumption of oats plus canary seed) were determined when juveniles were 10–12 (test 1), 20–22 (test 2) and 35–38 (test 3) weeks of age. Capped bars indicate 1 SE.

behaviour influences the food preferences of domestic chicks, *Gallus gallus* (Capretta 1977), and may be an important mechanism by which learned behaviour patterns are transmitted from parent to offspring in mammals (Galef & Clark 1971) and birds (Neuringer & Neuringer 1974).

Unlike the adult finches, juvenile birds never experienced negative consequences from eating oats and so had no aversion to them. Thus, when tested individually, juveniles responded by eating oats as well as canary seed, and preference for oats increased over time in the group not originally exposed to oats. The oat preference scores never reached the level of the group that was exposed early to oats, however, and this residual difference was attributable to the passive influence of the adult birds.

Conditions in this study provided a stringent test of effects of early dietary experience on subsequent seed preferences. (1) The test foods were always presented together, so the birds were free to choose oats or canary seed. (2) Daily access to test foods did not exceed 1 h during the first few weeks of life. (3) Test foods were then unavailable for 5–6 weeks until the initial preference test and were unavailable between tests. (4) Conditions for preference determinations were different from those in breeding cages, so conditioning to the experimental regime was unlikely.

Prior experience may be an important factor in individual food selection (Shettleworth 1987). My results indicate that food avoidance learning by adult house finches can affect dietary experience of dependent young. Furthermore, such early dietary experience affects food choices when the offspring are independent. This effect is achieved by experienced adult birds demonstrating what to eat, not what to avoid (Galef 1985; Avery 1994).

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