

Feeding neophobia and ecological plasticity: a test of the hypothesis with captive sparrows

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Abstract. The hypothesis that quantitative differences in neophobia underlie variation in ecological plasticity was tested by comparing feeding responses of wild-caught immature song, *Melospiza melodia*, and swamp, *M. georgiana*, sparrows in captivity. The song sparrow is a habitat generalist and good colonizing species, while the swamp sparrow specializes on marsh habitats. As predicted by the neophobia hypothesis, captive swamp sparrows showed a greater hesitancy to feed in the presence of a variety of novel objects than did song sparrows. Swamp sparrows made significantly more approaches to the food source without feeding when a novel object was present. There was a consistent difference in latency among individuals within each species. Habituation reduced latencies in the most neophobic sparrows, but sometimes almost a week of constant exposure was required before swamp sparrows fed without hesitation.

Some animal species appear to be more ecologically plastic than others, that is, more adaptable to a variety of habitats or food types (Miller 1956; Klopfer & MacArthur 1960; Morse 1980). This adaptability may allow species to colonize new habitats or use new resources (Miller 1956; MacArthur 1972; Yeaton & Cody 1977). Does ecological plasticity have an identifiable behavioural basis that can be measured in individual animals?

Because it will directly affect how an animal responds to new habitats or resources, the novelty response is a reasonable place to search for a psychological basis of plasticity. There is much evidence to suggest that a variety of animals respond differently to novel stimuli, often with fear and avoidance (Schleidt 1961; Corey 1978). Aversion to new microhabitats might restrict birds from taking advantage of new situations; reduced neophobia would allow greater opportunism. For neophobia to be an important determinant of interspecific differences in ecological plasticity, however, the intensity of response should vary consistently between individuals and species. Variation in fear of approaching novel objects to feed has been found among species and strains of *Rattus* (Mitchell 1976; Cowan 1977) reared under identical conditions.

Based on laboratory studies of two species of migratory warblers, I argued that differences in ecological opportunism observed in the wild (Greenberg 1984a) resulted from differences in feeding neophobia (Greenberg 1983, 1984b). Indi-

viduals of the more ecologically stereotyped species were consistently more hesitant to feed at a novel object. To test this hypothesis further, I selected two recently diversified species of sparrows in the genus *Melospiza* (Zink 1982). The song sparrow, *Melospiza melodia*, exhibits several features of its natural history that suggest it is a good colonizing species (Miller 1956): (1) it breeds throughout North America in a variety of scrub and marsh habitats (Aldrich 1984); (2) it is a common inhabitant of small islands (Yeaton & Cody 1977); and (3) it is a common commensal of humans, living in agricultural and suburban development. Miller (1956) argued that the plasticity of young dispersing birds in accepting a wide range of possible habitats may have been a driving force in the geographical diversification of this species. Similarly, Peters et al. (1980) related aspects of song learning to habitat plasticity of song sparrows. In contrast, the swamp sparrow, *M. georgiana*, has been cited as a habitat specialist, when compared with song sparrows. Except for periods of migration, swamp sparrows are found primarily in marshes or marsh-like habitats (Miller 1956; Wetherbee 1968).

Preliminary experiments with feeders in the wild showed that swamp sparrows avoid feeding in the presence of novel objects more frequently than do song sparrows (Greenberg 1989). The experiments reported here test the responses of captive yearling song and swamp sparrows to feeding in the presence of novel objects. Under captive conditions, social interactions can be eliminated and other factors

controlled. The degree of neophobia is measured as the latency to feed at a familiar food cup adjacent to a variety of presumably unfamiliar objects.

METHODS

Experiments were conducted on 11 first-year swamp sparrows (seven males and four females) and 10 song sparrows (seven males and three females), all captured in November 1986 during autumn migration. Age was determined by degree of skull pneumatization and sex was determined by laparoscopy following the experiment. All sparrows were kept in small single species groups in flight cages for at least a month before the experiments began. Experiments were conducted with birds housed in finch cages measuring $1.0 \times 0.6 \times 0.4$ m in a small room with acoustically tiled walls; the observer was located in an adjacent room separated by a one-way mirror window.

The reasoning behind the experiment was that a consistent response to a diversity of unusual objects is most parsimoniously explained by an overall novelty response, rather than differential reaction to a large number of particular stimulus features. The objects were made of artificial materials to minimize the possibility that they, or similar objects, had been experienced by the sparrows in the wild. The novel objects were identical to those used in previous field experiments and include: black box, a box measuring $10 \times 10 \times 25$ cm open at one end and covered with black construction paper; easter grass, a small clump of green and pink cellophane strips; tube, a section of mailing tube measuring 20×10 cm (laid flat); green spikes, six green pipe cleaners measuring 20 cm in a plasticine base; orange leaf, a single orange construction paper leaf measuring 10×20 cm attached to pipe cleaners and affixed to a Plasticine base; and tropical leaves, a cluster of green and maroon, vinyl leaves.

Experiments were conducted simultaneously on three sparrows that were visually isolated from each other. Each set of three consisted of one swamp and two song sparrows or, in alternating trial blocks, two song and one swamp sparrows. The sparrows were kept in the test room for 7 days before a series of control trials were conducted. The seven control trials measured the latency to feed at a small plastic cup measuring 2×2 cm filled with millet after 90 min of food deprivation. Median values for all individuals but one fell under 60 s. A single song sparrow that would not feed consistently

at the plain cup was excluded from further experiments.

Experimental trials were identical to control trials except that one of a set of six novel objects was placed next to the food cup. If a bird failed to feed in 20 min (1200 s), the object was immediately removed, and the latency to feed at the unadorned cup was measured. In all 19 cases (seven during the neophobia test and 12 during the habituation trials), the latency after removal was less than 30 s, suggesting that the disturbance of placing or removing objects per se was not responsible for the hesitation. The experimental room was not completely sound proof, very occasionally sparrows responded to noises in the building by freezing but appeared to recover abruptly from these periods by wing stretching and bill wiping. Because freezing occurred in response to other stimuli in discrete periods, I recorded the duration of these periods and removed them from the calculated latencies. A second measure of neophobia was the number of approaches before feeding. An approach was scored when a sparrow moved to within 7.5 cm of the food cup on the cage floor without feeding from the cup. This distance was selected because it is the approximate distance from which sparrows initiate strikes at the food cup.

Habituation to novel objects was studied in the three swamp sparrows with the greatest mean feeding latencies during the original neophobia test. Each was separately presented chenille stems, easter grass and a tube in their cage but away from their food for a week. They were deprived of food twice a day for 90 min, their food cup was placed next to the object and the feeding latency was timed. The experiment was conducted until feeding occurred in less than 60 s for four consecutive trials.

RESULTS

Latency

Swamp sparrows fed with greater latencies ($\bar{X} \pm \text{SE} = 494 \pm 90$ s) than did the song sparrows (131 ± 59 s; 1200 s was substituted for 'no feed'). However, latencies during control trials were somewhat greater in the song sparrows than in swamp sparrows (80 ± 1.5 s versus 43 ± 0.8 s). The pooled cumulative distributions for each species are shown in Fig. 1. Song sparrows showed a significantly greater latency for five out of six of the microhabitats (Mann-Whitney *U*-test; Table I). A repeated measures ANOVA was conducted using the

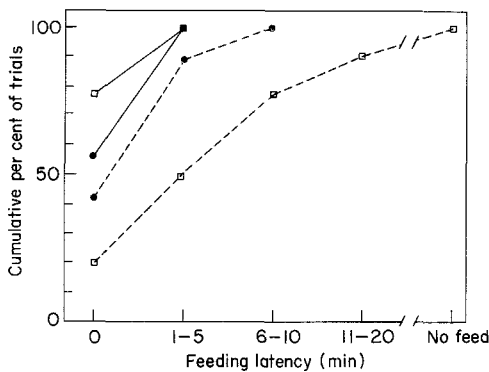


Figure 1. Cumulative distribution of latencies for experimental trials (---), when a novel object was placed next to the food cup, and control trials (—), when no object was present. Song sparrow is indicated by ● and swamp sparrow by □. Trials are pooled for all individuals within a species.

different objects presented to one individual as the repeated variable (SAS 1985). This analysis showed a significant difference between the latencies of the two species ($F_{1,18} = 9.51$, $P < 0.01$), a significant object effect ($F_{5,14} = 7.6$, $P < 0.01$), and no species \times object interaction ($F_{5,14} = 51$, $P = 0.76$).

Approaches

Latency was often accompanied by a generally high degree of arousal and excitement, particularly in swamp sparrows. During the latency period, individuals often approached the food cup and jumped back without feeding. This occurred with a mean frequency of 3.6 ± 0.7 approaches per trial in swamp versus 0.7 ± 0.2 per trial in song sparrows (Fig. 2, Table II). Approaches were always directed to the cup, and sparrows only rarely pecked or investigated the object. The difference between species was significant for four of six objects. A repeated-measures ANOVA was conducted using different objects presented to a single sparrow as the repeated measure. The analysis showed a significant difference between the species ($F_{1,18} = 12.8$, $P < 0.01$), but no significant variation between objects ($F_{5,14} = 1.13$), and no significant species \times object interaction ($F_{5,108} = 0.78$).

Individual Consistency

Individual sparrows showed an overall consistency in latency responses to the six microhabitats when compared with other individuals (Kendall's $W = 0.65$, $P < 0.001$); this is true even within species (Kendall's $W = 0.50$ and 0.49 , $P < 0.01$, for song and swamp sparrow, respectively). This suggests

Table I. Mean (\pm SE) of latency to feed (s) for individual song and swamp sparrows when a novel object was placed next to the food cup*

	Easter grass	Tube	Green spike	Tropical leaves	Black box	Orange leaves	Mean
Swamp sparrow	556 ± 97	508 ± 125	500 ± 158	330 ± 119	417 ± 86	209 ± 102	494 ± 83
Song sparrow	303 ± 56	95 ± 31	165 ± 64	90 ± 32	90 ± 20	38 ± 14	119 ± 28
P^\dagger	< 0.05	< 0.001	< 0.05	> 0.05	< 0.01	< 0.001	< 0.01

*The maximum value of 1200 s was substituted for no feed.

†Mann-Whitney U -test comparing species' medians.

Table II. Mean (\pm SE) for the number of approaches by sparrows to within 7.5 cm of the food cup

	Easter grass	Tube	Green spike	Tropical leaves	Black box	Orange leaves	Mean
Swamp sparrow	2.8 ± 0.8	5.0 ± 1.4	5.3 ± 1.9	2.5 ± 1.1	2.6 ± 0.9	3.1 ± 1.6	3.6 ± 0.7
Song sparrow	1.4 ± 0.5	0.9 ± 0.3	1.0 ± 0.4	0.3 ± 0.2	0.5 ± 0.3	0.7 ± 0.3	0.7 ± 0.2
P^*	> 0.5	< 0.01	< 0.01	< 0.01	< 0.01	> 0.05	< 0.01

*Mann-Whitney U -test comparing species' medians.

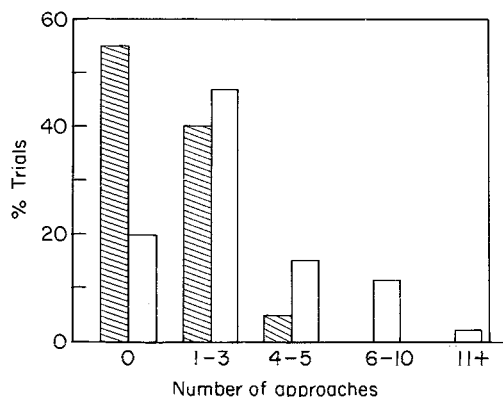


Figure 2. Distribution of trials with respect to the number of approaches made prior to feeding. Song sparrow is indicated by ▨ and swamp sparrow by □. Results are only for those trials during which objects were placed next to cup; there were no pre-feeding approaches recorded for either species during control trials. Results are pooled for all individuals of a species; for unpooled data see Table II.

that within species there were more and less neophobic individuals. The basis for this intra-specific variation is not clear. It is not based on sex in any obvious way: the three female swamp sparrows ranked second, third and eleventh based on their mean latency, and three female song sparrows

ranked first, fourth and sixth. Individual consistency was not found in the number of approaches (Kendall's $W=0.12$ for swamp and 0.26 for song sparrow, NS). The difference between the two measures of individual consistency may result from greater inclusiveness of the latency than the approach measure; approach is one of several activities that the sparrows performed during the latency period.

Habituation

The efficacy of habituation was demonstrated by further studies of three swamp sparrows with the greatest latencies in initial experiments. All three of the sparrows gradually reduced their feeding latencies from 'no feed' to less than 30 s (Fig. 3). These trials showed that reduction in feeding latency, even with continued exposure in a small cage, can take a long period. In only one case did one of three sparrows feed at an object during the initial trial of the habituation experiment. This suggests that there was little inter-object transfer of the effects of habituation.

DISCUSSION

These experiments established that sparrows from different species showed consistently different

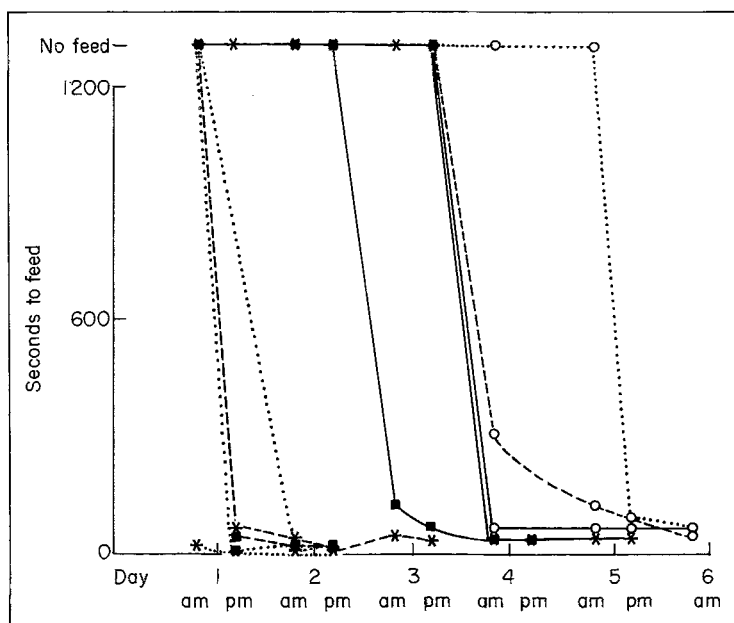


Figure 3. Feeding latency during repeated trials with one microhabitat. Each line represents an individual swamp sparrow's performance at one microhabitat over a series of trials conducted twice daily. Solid, dashed and dotted lines correspond to different individual sparrows.

latencies for feeding in the presence of novel objects and that this latency was much greater for swamp sparrows. The two species were represented by similar sex ratios so interspecific differences were not confounded by differences in sex. A difference in feeding latency between these two sparrow species does not appear to have resulted from a different motivation to feed, since swamp sparrows fed more rapidly in the control trials and approached the food cup more often before feeding in experimental trials than song sparrows. Experimental results suggested that inhibition to feed at objects was simply greater in swamp than song sparrows. This response was consistent over a variety of objects, suggesting that swamp sparrows respond differently to novel stimuli than do song sparrows. These results complement earlier field experiments (Greenberg, 1989) that showed a reduction of swamp sparrow (but not song sparrow) visitation to feeders when surrounded by novel objects. The field experiment established that the novelty response can be detected under more natural conditions while the laboratory experiment demonstrated that there was a quantifiable difference in the performance of individual sparrows of the two species under more controlled circumstances.

Although these experiments do not exclude the possibility that the degree of neophobia is a result of differences in experience prior to the experiments, the results suggest that, for whatever reason, dispersing immature song sparrows may be less inhibited by new situations than are individuals of its more specialized congener. Genetically based variation in neophobia, such as has been documented in rats (Mitchell 1976; Cowan 1977) is a possible mechanism to account for differences in the feeding response of the sparrows. Such quantitative differences in response provide a relatively simple mechanism whereby selection could shape ecological plasticity: this can be tested by conducting similar experiments on sparrows reared under identical laboratory conditions.

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