

ECOLOGICAL PLASTICITY, NEOPHOBIA, AND RESOURCE USE IN BIRDS

RUSSELL GREENBERG

Abstract. Determining the mechanisms that underlie ecological plasticity should be an important focus of avian behavioral ecology. Most attempts to model the responses of birds to changes in food distribution and abundance of potential competitors are based on the assumption that different species sample and track resources in an equivalent manner. However, differences in how readily birds respond to novel resources are difficult to model and may be impossible to predict based on strictly economic approaches. Most observers of wild birds have noted intrinsic differences within and between species in “ecological plasticity,” or the tendency to exploit new resources. Furthermore, it has been proposed that the degree of plasticity influences a species’ colonizing ability and, ultimately, the probability that it can give rise to other species occupying new adaptive zones. I propose that variation in plasticity is a direct result of variation in neophobia: the fear of feeding on new foods or approaching new situations. This provides natural selection with the raw material for adjusting adaptive levels of neophobia. Where ecological plasticity is favored, selection could act to reduce neophobia.

Key Words: Habitat selection; foraging; warbler; *Melospiza*; *Dendroica*.

Most field ornithologists possess an intuitive feel for the variation in ecological plasticity in species. Species, even closely related ones, often differ strikingly in the range of habitats occupied or foods taken. On the surface, it seems that this variation does not result entirely from differences in morphological adaptations, but also stems from differences in the psychological basis of decision-making.

Although there has been a long history of interest in ecological plasticity, its definition has been vague and has involved a blending of two rather distinct attributes: lack of specialization and flexibility in the face of change. Plasticity has most often been related to the lack of specialization, the observed ecological amplitude of a species (specialist versus generalist). Miller (1942), Klopfer and MacArthur (1960) and others have associated ecological plasticity with the breadth of resources and habitats used by a species. Klopfer (1967), for example, defined stereotypy (the opposite of plasticity) at the level of perception as “a sensitivity to, or an awareness of, or preference for, a limited range of a larger complex of stimuli.” He distinguishes this plasticity in preference from locomotory plasticity, which involves the lability of motor patterns used in searching and attacking prey. Since the ability to perform a variety of locomotory skills results from morphological specialization, it is probably best to consider preference, the focus of this paper, and locomotion separately (see Martin and Karr, this volume).

Plasticity is not simply an alternative term for the concepts of generalist versus specialist (Morse 1980a). What separates it is the second attribute, flexibility in the face of change. In general, plasticity can be defined as “the capacity of organ-

isms of the same (= similar) genotype to vary in developmental pattern, in phenotype, or in behavior according to varying environmental conditions” (Merriam-Webster 1986). This attribute of ecological plasticity, then, reflects a bird’s ability to respond to changes in food, competition environment, and the presence of novel resources. To separate the static concept of specialization from the dynamic concept of plasticity, Morse (1980a:12) constructed a two by two classification, with examples, based on degrees of ecological amplitude (specialist versus generalist) and ability to respond to changes in resources (stereotyped versus plastic). Although it is useful to divorce these two concepts, it is likely that there is a strong correlation between observed generalization and plasticity in birds. A thorough discussion of the relationship between ecological specialization and predictability through time can be found in Sherry (this volume).

At what level of biological organization should ecological plasticity be analyzed? With the exception of the experiments of Klopfer (1963, 1965, 1967), assessment of plasticity has been based generally on the performance of populations or species. However, if it is to be argued that variation in ecological plasticity is adaptive, then the ways by which plasticity is regulated in individuals need to be established. The purpose of this paper is three-fold: (1) to briefly establish the importance of the study of ecological plasticity of individuals to the understanding of the evolution and ecology of foraging behavior and habitat selection; (2) to propose the neophobia hypothesis as a mechanism for regulating the degree of ecological plasticity that characterizes a particular species of birds; and (3) to summarize

experiments that explore the comparative aspects of neophobia and relate these to the concept of ecological plasticity.

THE IMPORTANCE OF ECOLOGICAL PLASTICITY

ECOLOGICAL STUDIES

One of the major goals of community ecology is to develop a body of theory that will predict how animal populations respond to different levels of competition, predation, and other biotic interactions. The most unfortunate aspect of the science as it has been applied to birds is that its perspective often has been static, based on descriptions of community structure. Only occasionally have experimental manipulations of food abundance or competitive and predatory environments been attempted. Community dynamics are often inferred from natural experiments, such as differences between island and mainland communities (MacArthur and Wilson 1967; Crowell 1962; Morse 1971a, 1977; Diamond 1975; Yeaton and Cody 1977; Wright 1979; Keeler-Wolf 1986). Changes in foraging niche breadth have been cited as evidence for the importance of competition in restricting foraging variability. Some community theory predicts that as interspecific competition decreases and intraspecific competition increases, variation in resources used should also increase by a process known as character release (Diamond 1975).

The search for good examples of character release has been contentious, at best (Abbott 1980, Keeler-Wolf 1986). Although there appear to be a few species that occupy a greater range of habitats and microhabitats on islands than their mainland counterparts—Song Sparrows (*Melospiza melodia*) (Yeaton and Cody 1977), Bananaquits (*Coereba flaveola*), and Barred Antshrikes (*Thamnophilus doliatus*) (Keeler-Wolf 1986)—one cannot help but be impressed at the large number of species that show neither any documented character release nor density compensation (i.e., population increases in the absence of putative competitors). Do these instances where character release are not observed provide evidence that competition is not important, or do they indicate that there are intrinsic differences in the plasticity of the species involved? In his studies of small land-bridge islands in Lake Gatun, Panama, Wright (1979) found that the few species that remained on the smallest islands did not increase in abundance from mainland sites with literally hundreds more species. He attributed this to foraging stereotypy, which prevented tropical forest species from taking advantage of the greater abundance of insects

on the small islands. Keeler-Wolf (1986) also suggested that such stereotypy also characterized most tropical forest birds, preventing their opportunistic use of new microhabitats in the depauperate forests of Tobago. Morse (1971, 1980) hypothesized that bird species can be classified by the degree to which they are able to respond to new resources through learned or genetically based changes. He argued that the degree to which a bird's foraging decisions are genetically based, and not susceptible to modification by learning, will determine, in part, how readily it can colonize islands.

Related to this work on islands is the hypothesis that more stable environments, such as tropical rain forests, are populated by birds that are stereotypic specialists when compared to their temperate zone equivalents (Klopfer and MacArthur 1960). They argued that a fundamental difference in how habitat and foraging preferences are learned might account for the narrower and more stable niches of tropical forest birds.

EVOLUTIONARY HYPOTHESES

Behavioral plasticity has been implicated as being important in determining the probability that new adaptive zones, i.e., major shifts in the way of life of organisms, can be invaded during adaptive radiations. This idea has been the subject of general speculation, and not the focus of rigorous study, because it is hard to derive a measure of plasticity independent of the current distribution of a species. This lack of independence can readily lead to circular arguments.

Behavioral plasticity has long been suspected to be a moving force in the evolution of new morphological adaptations (Mayr 1974). Morgan (1896) described the relationship between plasticity and genetic evolution, arguing that somatic plasticity initially allows organisms to adapt to new environments, paving the way for genetically based adaptation to the new conditions. Hardy (1965) discussed the relationship between the adaptive foraging response of birds and the new selective environment this creates for bill morphology, and argued that specialization resulting from adaptive radiation is derived from behavioral shifts in a more generalized form.

That differences in plasticity play a key factor in the development of adaptive radiations has been suggested in several contexts. On the broadest taxonomic level, it has been argued that the rapid adaptive diversification found in birds and mammals, compared to other groups of vertebrates, is related to variation in behavioral plasticity. This may be related to larger relative brain size and the greater degree to which social learn-

ing is important in higher vertebrates (Wyles et al. 1983). In this case, Wyles et al. have focused less on how new resources are discovered by individuals and more on how novel behaviors spread through populations via social learning.

The comparison of intrinsic differences in the biology or behavior of major classes of organisms that might contribute to rapid evolutionary rates is interesting, but also unsatisfying. There are too many other differences between groups to easily tease out factors relating solely to behavioral plasticity. The comparative approach based on closely-related species, however, is often useful in narrowing the possible factors effecting variation in traits (Kamil and Yoerg 1982, Clutton-Brock and Harvey 1984). Morse (1980) has argued that at least within major groups, such as birds, plasticity may vary considerably at the interspecific level so that generalizations focused on major taxa may be unfounded.

The relationship between ecological plasticity and adaptive radiation has rarely been explored. Miller (1942, 1956) repeatedly suggested, using species of sparrows in the genus *Melospiza* as an example, that there is a relationship between ecological plasticity, in this case the probability of invading new habitats, and the degree of geographic variation found in a species. In their taxon cycle model, Ricklefs and Cox (1972) proposed a pattern of evolution of island forms (based on the West Indies) in which species with general adaptations invade islands and give rise to increasingly specialized species. Although not a focus of the discussion, the model suggests that ecological plasticity should decrease as adaptive radiation progresses on archipelagos.

It is possible that hypotheses regarding the role of ecological plasticity in adaptive radiation can be tested by examining the relationship of plasticity, as a character, with a known phylogeny. However, without the ability to assess plasticity as a specific character, these hypotheses will remain circular. In the next section I will argue that variation in neophobia may provide at least one important trait associated with plasticity that can be tested in individual birds.

THE NEOPHOBIA HYPOTHESIS

A potentially simple mechanism to regulate the degree of ecological plasticity might be found in a generalized response to new stimuli (Berlyne 1950, Glickman and Sroges 1966, Barnett and Cowan 1976, Cowan 1977). In birds, novelty responses have been best established for reactions to potential predators. Schleidt (1961) found that the response of young turkeys to silhouettes passing was largely dependent upon the object's unfamiliarity. Novelty also plays a role in the

type of food birds will eat (Coppinger 1970, Greig-Smith 1987) as well as the site or container at which birds will forage (Greenberg 1983, 1984a, b, c, 1988). The introduction of novelty generally provokes a differential response, either neophilia (attraction) or neophobia. In adult foraging sparrows and warblers I have found the response to be neophobic (Greenberg 1983).

Laboratory experiments have also shown that birds avoid eating novel foods or eating from novel microhabitats (Coppinger 1970, Greenberg 1984c, Greig-Smith 1987). But the response appears to be much more than passive avoidance. Most often, these birds approach and withdraw repeatedly from the aversive feeding situations. Coppinger also noted that birds were often excited in the presence of an unfamiliar food item. I applied the generally used label neophobia (Barnett 1958) because the avoidance of feeding on novel foods or at novel microhabitats is not simply a matter of passive preference but seems to be associated with an acute stress response, a syndrome of physiological responses known as the fight-or-flight response (Coppinger 1970). In other animals novelty responses have produced physiological responses correlated with acute stress, such as the increase of circulating corticosteroids, which can be mitigated through avoidance behavior (Misslen and Cigrang 1986).

Based on the role of neophobia in causing avoidance of new feeding situations, I have developed the neophobia hypothesis (Greenberg 1983, 1984a, b, c) which is:

- (1) Birds are able to respond to novel stimuli.
- (2) Birds often respond with acute stress, which leads to avoidance and excitement.
- (3) The attraction of a potential food source and the fear response produce a tension, which is ultimately resolved either through habituation to the novel stimulus or by avoidance of it. The greater the intensity of the original fear response to novel stimuli, the less likely the individual will explore or feed at the novel stimuli.
- (4) The fewer novel microhabitats or foods the bird approaches, the fewer new opportunities will be available for its foraging repertoire. The result will be reduced ecological plasticity.
- (5) Novelty responses do not provide a rigid barrier but a brake that slows foraging niche expansion. Novelty responses can be reduced through habituation.
- (6) Neophilia in juvenile birds makes this period particularly important in shaping the foraging niche of a species (Greenberg 1984c). The more neophobic the species, the more important early experience during the period of parental care will be. This is because neophobic responses should protect preferences from change due to

TABLE 1. MEAN NUMBER OF APPROACHES AND FEEDING ATTEMPTS AT TEN OBJECTS WITH HIDDEN MEALWORMS (GREENBERG 1983)

	No. of foraging attempts	No. of approaches	No. of weak approaches ^a
Chestnut-sided Warbler	1.0 ^b	5.6	1.7 ^b
Bay-breasted Warbler	4.0	5.5	0.3

^a Weak approaches involved birds that came no closer than 7.5 cm to the object.

^b Interspecific difference significant $P < 0.05$ based on Mann-Whitney test.

associative learning (for a discussion of the role of neophobia in limiting learning ability in rats see Holson 1987).

That a neophobic response can affect the evolution of ecological plasticity is clear. Differences in neophobia between laboratory and wild strains of rats and among breeds of dogs, for example, suggest that enough heritable variation in the novelty response exists for artificial selection to shape major differences (Barnett 1958, Barnett and Cowan 1976, Mitchell 1976).

Although a neophobic response potentially can play an important role in determining differences in plasticity, how can it be distinguished from the overall response that animals could have to any feeding situation? Many foraging decisions are probably marked by some ambivalence. Birds are attracted to a particular location based on direct observation of food, expectations derived from past experience, or the presence of other birds. But the presence of predators or competitors adds risk, and may discourage birds from visiting an otherwise attractive site. This continual ambivalence has been the subject of intense study by workers interested in the trade-offs between risk and energy reward in sparrows feeding away from shrubbery, for example (Grubb and Greenwaldt 1982, Schneider 1984). By keeping the expected energy gain constant, but moving the food with respect to cover, one can infer the relative role of fear of predation in shaping the decisions of sparrows. In a similar manner, the role of fear of novelty can be explored by manipulating novelty while keeping expected gain constant.

In the experiments described below, I assumed that by presenting food to hungry birds in a conspicuous and familiar manner the attraction of a feeding site could be adjusted sufficiently high that its contribution to variation in feeding rate is insignificant. Differential latency to feed when novelty is imposed can be safely attributed to an aversion, and the experiment need only distinguish exactly what causes the aversion.

The problem of inferring the experience of wild-caught birds can be obviated by rearing birds

under controlled conditions. However, it is more practical to assay the response of wild-caught birds and I have inferred differences in neophobia by presenting them with a wide range of objects unlikely to have been seen previously. These objects are characterized by many types of stimuli. If the birds respond with consistent aversion to all of the various objects, then it is unlikely that the experiments are distinguishing an innate response to a particular stimulus. A consistent response can most parsimoniously be ascribed to a generalized novelty response.

Because the experiments encourage or force the subjects to confront the potentially aversive objects, differences in latency or any other measure can only be compared qualitatively within the experimental paradigm. The fact that it may take one individual only 20 min and another only a minute does not mean that the former would visit the aversive object rapidly in the wild. Further, the objects are selected to be highly divergent from what is normally encountered and may produce aversions greater than one would see from natural habitat features.

EXPERIMENTS WITH WARBLERS

I studied two species of *Dendroica* warblers that winter in Central Panama (Greenberg 1984a). The fact that I could study them in sympatry is important, since the attributes of specialization and plasticity are relative; only by comparing the response of species to the same resources can comparisons be made. Based on my observations during the three winters, and others made by Morton (1980a), I concluded that Bay-breasted Warblers (*D. castanea*) were more flexible and generalized in their foraging behavior than Chestnut-sided Warblers (*D. pensylvanica*). Often Bay-breasted Warblers displayed a high degree of opportunism, feeding on insects attracted to lights, garbage cans, sewage outfalls and dog food dishes. In forests Bay-breasted Warblers were the most variable and generalized of the small foliage-gleaning birds with respect to foraging height, substrate, and gross diet composition (fruit versus insects). Chestnut-sided Warblers consistently ranked as the most specialized.

To study the mechanisms that regulate the degree of apparent plasticity in the two species, I observed the responses of immatures, captured in autumn migration, to novel feeding situations presented in captivity (Greenberg 1983, 1984b).

The first experiment explored how individuals of the two species responded to presumably novel microhabitats that contained hidden prey. Under these circumstances both the intrinsic attractiveness and aversiveness were operating to determine the ultimate success of the bird approaching and capturing the prey. A series of 10

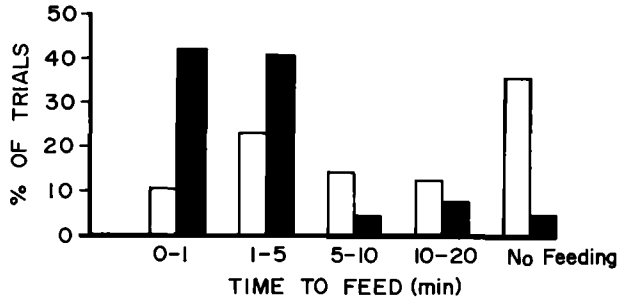


FIGURE 1. Percentages of trials in which Bay-breasted (black bars) and (white bars) Chestnut-sided Warblers took various time intervals to feed. Experiment is the pooled result of eight Bay-breasted and seven Chestnut-sided Warblers offered food at eight different microhabitats. The Chestnut-sided Warblers took longer to feed at all microhabitats. Control trials with no objects averaged less than 30 s for both species.

objects was presented in the home cage of the warblers for 10 minutes, and the numbers of approaches, close approaches, and prey captures were recorded. Although the two species approached a similar number of objects, the Bay-breasted Warblers approached more closely and captured the prey four times more often than did the Chestnut-sided Warblers (Table 1). The actual behavior of the two species seemed even more revealing: Chestnut-sided Warblers approached with a great amount of ambivalence—continually approaching and withdrawing—which was not observed in the Bay-breasted Warblers.

The second experiment introduced the strategy of reducing the uncertainty regarding the intrinsic attractiveness of an object by first depriving the birds of food and then presenting them with a conspicuous food reward (a cup of mealworms). Control trials consisted of presenting the food without the cup and the warblers fed rapidly during these trials (<30 s). A long latency was attributed to the response of the birds to the objects placed next to the familiar food cup. The data showed that regardless of what the object was, Chestnut-sided Warblers took much longer to feed at novel objects than did Bay-breasted Warblers (Fig. 1).

Additional experiments demonstrated that:

(1) The increased latency of the Chestnut-sided Warblers was not due to an increase in their exploratory behavior of the novel objects (i.e., greater "curiosity" in the Chestnut-sided Warbler, Greenberg 1984b).

(2) Naive Chestnut-sided Warblers distinguished objects that they were reared with versus novel objects up to four months after the rearing period (Greenberg 1984c).

(3) Increased hunger and interspecific social stimulation did not decrease the degree of neophobia shown by Chestnut-sided Warblers

(Greenberg 1987). Repeated short-term exposure did decrease the latency to feed at novel objects.

EXPERIMENTS WITH SONG AND SWAMP SPARROWS

The experiments with warblers provided the basis for the Neophobia Hypothesis. The experiments I have performed on *Melospiza* sparrows were the first prospective test of one of the major predictions of the hypothesis: a more generalized species should show consistently lower aversion to feeding in the presence of novel objects than a more stereotyped congener.

A prediction was made that the Swamp Sparrow (*M. georgiana*) should be more neophobic than the apparently more generalized and adaptable Song Sparrow (Miller 1956, Wetherbee 1968, Peters et al. 1980), despite their close phylogenetic affinity (Zink 1982). Song Sparrows occur in a wider range of scrub and marsh habitats (Morse 1977, Yeaton and Cody 1977), they are common colonists of small oceanic islands with a variety of habitats, and they occur commonly as a commensal with human. Swamp Sparrows are more restricted to shrub-marsh habitats.

One of the advantages of working with sparrows over most warblers is that they can be baited into feeders in the field. I exploited this to conduct experiments on novel object reactions both in the field and in the lab. The two approaches are complementary: field experiments remove the possibility that the responses are a result of stimulus deprivation and do not reflect responses of birds in the "real world." Caged experiments allow for individual testing of subjects under more controlled conditions.

Field experiments (Greenberg, 1989) were conducted by color-banding sparrows at a marsh along the Potomac in Alexandria, Virginia. After a regular group of Song and Swamp sparrows

TABLE 2. THE NUMBER OF VISITS/30 MIN TO A FEEDING STATION BY SONG AND SWAMP SPARROWS WHEN SURROUNDED BY NOVEL OBJECTS COMPARED WITH PAIRED CONTROL PERIODS

Object	Song		Swamp	
	Control	Experimental	Control	Experimental*
Black box	30	20	21	1
Easter grass	22	17	7	0
Tropical leaves	24	29	49	17
Tube	30	25	45	21
Green spikes	42	35	28	7
Orange leaves	29	30	18	9
Totals	177	156	168	55

* Difference between experimental and control in Swamp Sparrow is significant based on Wilcoxon paired-rank test ($t = 0$, $P < 0.025$).

was established at the feeders, I placed replicates of novel objects in a circle 0.5 m from the feeder. The feeder was watched for 30 min with the objects and 30 min without the objects, with the control and experimental periods alternated. Bird seed was added prior to each observation period. The number of individual visits was recorded for each species for each period (Table 2). Both predictions of the neophobia hypothesis were confirmed: (1) Swamp Sparrows visited the novel objects less often than the unadorned feeder, whereas there was no significant difference in Song Sparrows; and (2) the difference between the two species was consistent over all of the objects.

Individually housed immatures of both species were tested the next winter in a manner similar to the warbler experiments. Although the Song Sparrows averaged slightly slower in its foraging latency at plain cups (controls), they were consistently and significantly faster than Swamp Sparrows during the experimental trials with novel objects (Table 3). Swamp Sparrows also approached the cup more often prior to feeding

than did the Song Sparrows. The hesitancy disappeared in the Swamp Sparrows when they were repeatedly exposed to the objects.

DIRECTIONS FOR FURTHER WORK ON THE NEOPHOBIA HYPOTHESIS

Experiments to this point have established that novelty is an important factor underlying differences in plasticity between some species. Since large variation is found between closely-related species, and within species, in the case of rats and dogs, differences in ecological plasticity caused by changes in novelty responses may have the capability of rapid evolution. If so, closely-related species that rely upon more stable resources should forage more conservatively and hence be more neophobic.

However, these experiments do not yet establish neophobia as a general mechanism for regulating ecological plasticity. The following points might be addressed in future studies:

(1) The physiological correlates of feeding aversion need further work to see if variation in novelty responses are associated with elevated heart rate and circulating steroid levels, which would suggest that the acute stress responses are operating. Experiments could then examine whether interspecific variation in neophobia is correlated with the degree of change in these factors.

(2) Captive experiments with naive birds (Greenberg 1984c) should be pursued to determine if there is a genetic basis to the interspecific differences in neophobia.

(3) Further work should bridge the gap between the qualitative results obtained from the experiments employed so far and the magnitude of the effect of novelty under more natural conditions. This is important for applying this concept to field studies of foraging, since the results of laboratory and feeder studies can only be used

TABLE 3. MEAN LATENCY (SEC) AND NUMBER OF APPROACHES PRIOR TO FEEDING FOR 11 SWAMP AND NINE SONG SPARROWS FEEDING WHEN NOVEL OBJECTS WERE PLACED NEXT TO THE FOOD CUP

	Object						
	Easter grass	Tube	Green spikes	Tropical leaves	Black box	Orange leaves	No objects
Song Sparrow							
Latency ^a	304	95	165	90	90	38	80
Approaches ^b	1.4	0.9	1.0	0.3	0.5	0.3	0
Swamp Sparrow							
Latency	556	508	500	330	417	209	43
Approaches	2.8	5.0	4.4	2.5	2.6	3.1	0

^a Two-way ANOVA produced a significant species effect $F_{1,98} = 26.7$, $P < 0.0001$.

^b Two-way ANOVA produced a significant species effect $F = 20.1$, $P < 0.001$.

to compare species in a qualitative sense. Because novelty responses are easily measured, they can be used in a wide variety of experimental studies to test hypotheses concerning the adaptive significance and evolutionary and ecological consequences of differences in plasticity.

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