Stenning, M. J., 1996, Hatching asynchrony, brood reduction and other rapidly reproducing hypotheses, *TREE* **11**:243–246.

Stephens, D. W., and Krebs, J. R., 1986, *Foraging Theory*, Princeton University Press, Princeton NJ.

Stolason, S. H., and Beissinger, S. R., 1997, Hatching asynchrony and the onset of incubation in birds, revisited; when is the critical period?, *Curr. Ornithol.* **12**:191–271.

Teather, K. L., 1987, Intersexual differences in food consumption in hand-reared Great-tailed Grackle (*Quiscalus mexicanus*) nestlings, *Auk* **104**:635–639.

Teather, K. L., 1992, An experimental study of competition for food between male and female nestlings of the Red-winged Blackbird, *Behav. Ecol. Sociobiol.* **31**:81–87.

Teather, K. L., and Weatherhead, P. J., 1988, Sex-specific energy requirements of Great-tailed Grackle (*Quiscalus mexicanus*) nestlings, *J. Anim. Ecol.* **57**:659–668.

Trivers, R. L., 1974, Parent-offspring conflict, *Am. Zool.* **14**:249–264.

Verhulst, S., and Wiersma, P., 1997, Is begging cheap?, *Auk* **114**:134.

Weatherhead, P. J., 1985, Sex ratios of Red-winged Blackbirds by egg size and laying sequence, *Auk* **102**:298–304.

Weathers, W. W., Hodeum, P. J., and Anderson, D. J., 1997, Is the energy cost of begging by nestling passerines surprisingly low?, *Auk* **114**:133.

Westneat, D. F., Clark, A. B., and Rambo, K. C., 1995, Within broad patterns of paternity and paternal behaviour in Red-winged Blackbirds, *Behav. Ecol. Sociobiol.* **37**:349–356.

Wiehe, K. L., and Bortolotti, G. R., 1992, Facultative sex ratio manipulation in American Kestrels, *Behav. Ecol. Sociobiol.* **30**:379–386.

Winkler, D. W., and Adler, F. R., 1996, Dynamic state variable models for parental care: I. A submodel for the growth of the chicks of passerine birds, *J. Avian Biol.* **27**:343–353.

Wright, J., 1998, Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging, *Behav. Ecol. Sociobiol.* **42**:423–429.

Wright, J., and Cuthill, I., 1990, Biparental care: short-term manipulation of partner contribution and brood size in the Starling, *Sturnus vulgaris*, *Behav. Ecol.* **1**:116–124.

Zahavi, A., 1975, Mate selection—a selection for a handicap, *J. Theor. Biol.* **53**:205–214.

Zahavi, A., 1977, Reliability in communication systems and the evolution of altruism, in: *Evolutionary Ecology*, (B. Stonehouse, and C. M. Perrins, eds.), Macmillan, London, pp. 253–259.

Zahavi, A., and Zahavi, A., 1997, *The Handicap Principle: A Missing Piece of Darwin's Puzzle*, Oxford University Press, Oxford.

CHAPTER 3

ECOLOGICAL ASPECTS OF NEOPHOBIA AND NEOPHILIA IN BIRDS

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1. INTRODUCTION

1.1. The Implications of Novelty Responses and Exploration: A Brief Overview

Nearly fifty years ago D. F. Berlyne (1950) wrote

> Psychology has so far had surprisingly little to say about stimuli which influence behavior simply because they are new. Stimuli which owe their potency to the fact that they are not new ... have given rise to the vast corpus of observations and generalization that go to make up learning theory. But the everyday activity of both men and animals seem [sic] to attest to the importance of novelty as well as familiarity in features of the environment.

This reticence may have ended long ago for psychology and ethology (Corey, 1977); novelty is a recurrent theme of studies of a variety of behavioral processes (Thorpe, 1956; Berlyne, 1950) such as filial im-

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printing (Bateson, 1971), responses to overflying objects (Schleidt, 1961), and taste aversion learning (Corey, 1977; Shettleworth, 1972).

Still, the terms "ecology" or "behavioral ecology" could be substituted for "psychology" in the Berlyne quotation and retain its accuracy. In these fields, theories aimed at predicting foraging preferences and habitat selection have flourished with, at best, only passing reference to the response of animals to novelty. Derived from models of human microeconomics mixed with some concepts of comparative cognitive psychology, these theories seek to predict an animal's decision in the face of familiar resources (Stephens and Krebs, 1986; Rosenzweig, 1985). In nature, however, many of the decisions that animals make involve resources that are qualitatively novel and to varying degrees dissimilar from what they have previously experienced. Novelty is a unique transitory quality based on the experience of the individual and not on the intrinsic value or danger of the novel object itself. Therefore, it would seem to be both necessary and challenging to incorporate novelty into models of animal decision-making (Greenberg, 1983).

"Novel" versus "familiar" is a fundamental way by which vertebrates classify objects, and the form of novelty responses varies far less than their intensity. What has made responses to novelty such a compelling focus of study for both comparative psychologists (Berlyne, 1950) and ethologists (Thorpe, 1956), and should make their study a key issue for ecologists, is that these responses form a universal solution to so many problems facing animals. Novelty in foraging ecology and habitat selection is associated with a number of different phenomena. These include the appearance of a new prey type which has a bold and unusual color pattern; the seasonal progression of fruits, flowers, and vegetative structures; new habitats encountered because of seasonal migration and dispersal; and, more important, environments produced by rapid anthropogenic changes.

The relationship between learning mechanisms and the ecology of particular species has become an increasingly important area of research (Shettleworth, 1993; Tamil and Yoerg, 1982; Johnston, 1981). This research focuses primarily on cognitive processes. Yet before the costs and benefits of using an unfamiliar food or feeding site can be assessed by a bird, the food or site needs to be approached, explored, and sampled. The manner in which birds respond to unfamiliar stimuli is paramount in any learning process. However, emotional responses to the unfamiliar are often considered to be experimental artifacts that need to be eliminated through pre-training, or to be controlled; the quest is thought to be the elucidation of deeper learning and cognitive processes, rather than of behavioral patterns that are a significant aspect of

learning processes in their own right (Seferta, 1998). In other words, in our studies of avian cognition we may sometimes commit the "Oz Fallacy," i.e., mistaking courage for brains. Thus, for example, Seferta (1998) found that the apparent difference in the speed at which two dove species learned a simple task was related not to a difference in learning ability, but to fear of a novel situation, that is, to neophobia (Seferta, 1998).

Neophobia and exploration are integrally related to ecological plasticity (Morse, 1980; Klopfer, 1967), opportunism, or innovative behavior (Lefebvre et al., 1997)—phenomena that probably are driving forces in avian evolution (Wyles et al., 1983). After all, new niches are explored and incorporated through simple shifts in behavior long before morphological adaptations can be fine-tuned through natural selection. Such shifts are more likely to take place in species exhibiting ecological plasticity. Levins and Lewontin (1985) called for greater emphasis in evolutionary biology on the reciprocal interaction of environment and organism, noting that to a great degree animals shape their environment. Nowhere is the dialectical relationship between birds and their environment in greater relief than in the way that they seek out, explore, and ultimately respond to new habitat features, foods, and other potential resources.

Ecological stereotype (Morse, 1980; Klopfer, 1967), at the opposite end of a continuum from plasticity, describes the behavior of a bird (or other animal) that remains specialized even in the face of environmental changes. Such stereotypy may, in part, be enforced by the aversion with which individuals respond to novelty (Greenberg, 1990b). However, it is a legitimate question whether a generalized ecological stereotypy-to-plasticity axis—one that cuts across diverse categories of decision from diet selection to habitat preference—does in fact exist or is simply the investigator's reification of a heterogeneous mosaic of traits. If ecological plasticity and stereotypy are indeed traits with identifiable physiological underpinnings, this would have relevance to other fields, particularly conservation biology: The capacity for behavioral flexibility in the face of new or changing habitats and food sources may help determine how species adjust to anthropogenic changes (Greenberg and Droege, 1999; Morton, 1998). Therefore, it is more critical than ever to understand why some birds seem, at least, to be highly stereotypic while others show ecological plasticity.

Owing in part to the mobility of birds, novelty may play a particularly important role at critical junctures in their lives. The importance of neophobia in the foraging of adult birds has been well studied in a variety of taxonomic groups (Table I), including domestic and wild-type Mallards (*Anas platyrhynchos*; DesForges and Wood-Gush, 1975), Snail

TABLE I
Design, Setting, Taxonomic Focii, and Hypotheses for Published Studies of Exploration and Neophobia in Birds

Taxa	Comparison	Novel stimulus	Measures	Hypothesis	Naïve/ wild	Field/ lab	Reference
Mallard *Anas platyrhynchos*	Domestic and wild strains	Novel objects placed beside food	Latency to feed	Domestic strains are less neophobic	N	L	Desforges and Wood-Gush, 1975
Snail Kite *Rostrhamus sociabilis*	None	Unfamiliar snail species (food item)	Snail species consumed	Unfamiliar species is avoided	W	F	Beissinger *et al.*, 1994
American Kestrel *Falco sporverius*	None	Objects	Frequency of interaction	Juveniles prefer playing with objects similar to natural prey	N	L	Negro *et al.*, 1996
Domestic chicken *Gallus domesticus*	Cocks/capons	Objects, dyed food	Latency and duration of feeding	Testosterone influences neophobia	N	L	Jones and Andrew, 1992
Domestic chick	None	Video images	Latency to approach, duration of approach	Preference for familiar image	N	L	Jones *et al.*, 1996
Domestic chick	None	Object	Latency to approach	Prior experience influences latency	N	L	Saegert and Rajecki, 1973
Wood warblers *Dendroica* spp.	Interspecific	Series of objects + food	Latency to approach	Specialist is more neophobic	W	L	Greenberg, 1984b, 1983
Bananaquit *Coereba flaveola* and Lesser Antillean Bullfinch *Loxigilla noctis*	Interspecific	Novel objects near feeder	Latency and frequency of visits	Diet specialist is more neophobic	W	F	Webster and Lefebvre, 2000
Sparrows *Melospiza* spp.	Interspecific	Objects/food in novel container	Latency and frequency of approach	Specialist is more neophobic	N/W	F/L	Greenberg, 1990a, 1992, 1989
Zebra Finch *Taeniopygia guttata*	Solitary versus groups	Feeders/objects	Latency to feed	Social facilitation reduces neophobia	N	L	Coleman and Mellgren, 1994

Kites (*Rostrhomus sociobilis*; Beissinger et al., 1994); domestic chickens (*Gollus domesticus*; Murphy, 1977), Zenaida Doves (*Zenaido ourita*; Seferta, 1998), Barn Owls (*Tyto alba*; Schaden, 1993), Common Ravens (*Corvus corax*; Heinrich et ol., 1995), Blue Jays (*Cyonocitto cristata*; Coppinger, 1970), Coal Tits (*Porus ater*; Grünberger and Leisler, 1990), Moustached Warblers (*Acrocephalus melonopogon*; Raach and Leisler, 1989), European Robins (*Erithocus rubicolo*; Marples et al., 1998), European Blackbirds (*Turdus merula*; Marples et al., 1998), Northern Mockingbirds (*Mimus polyglottos*; Barrows et al., 1980), European Starlings (*Sturnus vulgaris*; Greig-Smith, 1987b), various Parulidae (Greenberg, 1983) and various sparrows (*Melospizo* spp.; Greenberg, 1989), Chaffinches (*Fringilla coelebs*; Marler, 1956), House Sparrows (*Passer domesticus*; Rana, 1989), and Zebra Finches (*Toeniopygia guttota*; Coleman and Mellgren, 1994).

The apparently opposite phenomenon from neophobia is neophilia, or the exploration of novel objects, and it too has been well documented across a broad taxonomic spectrum of birds (Ortega and Bekoff, 1987), particularly raptors, parrots, and passerines. However, the behavior of juveniles has been primarily reported. Young birds are more commonly attracted to approach and manipulate objects, and this tendency is less prone to extinction in them than in adult birds (Marchetti and Price, 1989; Vince, 1960). In adults, exploration of novel objects and visual patterns has been documented for Common Quail (*Coturnix coturnix*), Jackdaws (*Corvus monedula*; Wünschmann, 1963), parrots (Psittacidae; Mettke 1995; Deckert and Deckert, 1982), and woodpeckers (Picidae; Kilham, 1974).

The study of responses to novel objects and foods, rather than simply to new space, has been the focus of most research in birds (but see Verbeek et al. 1994; and Katzir, 1982). It remains an open question to what degree avian responses to novel objects are relevant to larger-scale issues of habitat selection. However, we suggest that responses to particular objects provide an appropriate scale at which to initiate the investigation of ecological plasticity. Many birds select their macrohabitat only a few times during a year or even a lifetime. In contrast, the decision to approach or not to approach an object that is a particular local feature of the habitat is made thousands of times a day, and it is the constellation of these decisions that is the basis for our concept of ecological stereotypy or plasticity.

1.2. Definitions

Because our subject is an area of research that may be unfamiliar to many ornithologists, we here briefly define some of our terms. *Novelty* is that which is both new and surprising (Barrows, 1995; Immelmann and Beer, 1989). Because animals can form generalizations that group stimuli into categories, the concept of novelty must incorporate the degree of dissimilarity and discontinuity from situations or objects that have been experienced before. *Neophobio* is the avoidance of an object or other aspect of the environment solely because it has never been experienced and is dissimilar from what has been experienced in the individual's past; the concept is associated with fear and the physiological and behavioral correlates of fear responses.

Exploratory behavior is "an animal's searching for and active investigation of novel situations in the absence of pressing physiological need" (Immelmann and Beer, 1989). This definition is centered on the exploration of novelty, but other definitions (see Barrows, 1995) take account of the possibility that familiar objects will continue to elicit exploration from time to time. This latter aspect of exploration is tantamount to sampling behavior, a concept that is commonly incorporated into standard analysis of foraging theory (see also Inglis and Shepherd, 1994). For this chapter, we use *neophilio* to describe instances of exploration in which investigation is elicited by an object's novelty.

The result of exploration is a reduction of the initial novelty responses, a form of habituation (Thorpe, 1956) that we will term *familiorizotion*. In addition to leading to familiarization, exploratory behavior may provide information about objects or places through *associotive* (trial-and-error) *learning*. Or exploration may provide information that, while lacking immediate utility, benefits the exploring animal in the future, a process known as *latent learning* (Renner, 1988).

1.3. Costs and Benefits of Neophilia and Neophobia

The primary benefit of exploration of novel objects is acquisition of information, such as whether an object can be approached without consequence (familiarization), or whether the object is or may in the future be a profitable resource (associetive and latent learning). Environmental uncertainties and resource requirements determine the value of information for eech individual. The value of information is the difference in payoff between the decision of an individual when it is informed and when it is uninformed (Gould, 1974). Therefore, the ultimate test of the value of exploration should be comparison of the performance at various tasks by individuals with exploration experience and those without that experience. This kind of test has not been performed for the type of exploration this chapter discusses. However, the value of exploration has on occasion been quantified for other behavior. For example, Stamps (1987) found that success in acquiring territories was higher in

lizards that could visually collect information about neighboring territories and their inhabitants than in lizards that could not.

Exploratory behavior also incurs costs; hence the benefits of neophobia. First, there is risk because an unknown object may harbor unknown predators, and an unknown food may be poisonous. Exploration also may cause a bird to be less vigilant as it undertakes an intense examination of objects (Lima and Dill, 1990). Additionally, exploration consumes time and energy, resulting in opportunity costs when birds explore unfamiliar objects that yield no immediate payoff while forgoing examination of familiar food sources. Once again, costs will vary with the age and condition of individuals and the foraging ecology and life history of their species.

Ultimate explanations for variation in novelty responses, particularly neophobia, have focused solely on either the cost or benefit of the ecological ledger. One dominant concept is that the relative danger of a species' environment will determine the level of exploration and neophobia. Animals that are likely to encounter unpredictable dangers (predation, poison, trapping, etc.) associated with foraging are partly protected by their increased caution in the face of novel foods or new feeding situations. This hypothesis underlies work on comparative neophobia in rats (Mitchell, 1976; Cowan and Barnett, 1975), which demonstrates that wild species or strains show higher degrees of neophobia than their domesticated relatives. Heinrich et al. (1995) proposed that the danger of foraging on exposed carrion is the underlying cause for the greater neophobia of Common Ravens as compared to other corvids. Species facing predation risk should explore changes in their environment less than those occupying safer environments.

Similarly, species living in environments in which food is more likely to be poisonous should be less exploratory and more neophobic than those in environments with a greater abundance of palatable foods (Galef and Clark, 1971). On the other hand, as a way of avoiding potentially noxious prey, neophobia carries a large potential cost. Birds have been shown to hesitate to attack a prey item simply because of its novel appearance (Vaughn 1983; Coppinger, 1970, 1969). In this way, neophobia in predators can be a critical behavioral component of apostatic selection in their potential prey (Allen, 1988, 1994), favoring a new prey phenotype just because it is rare. Mechanisms that allow avian predators to overcome this effect of neophobia would give them a behavioral weapon in the predator–prey arms race.

An alternative to the hypothesis that gives primacy to danger is that the degree of exploration and neophobia is determined primarily by potential benefits. Generalist species or those facing highly variable resources will gain more from reduced neophobia and greater explora-

tion than will more specialized species or ones that rely on more stable resources. The degree of specialization may in turn be determined by the level of morphological commitment to a particular niche as well as by the intensity of interspecific competition. Species showing less morphological or behavioral specialization for a particular mode of foraging can exploit more food types and foraging sites and should therefore show greater exploratory tendencies and reduced neophobia (Greenberg, 1983).

Factors affecting the value of information gathered from exploration include those that are intrinsic to the bird (morphological and other features that favor or disfavor ecological generalization) and those associated with the bird's relationship to its environment. As an example of the latter point, at the macrohabitat level the probability of discovering new resources through exploration is higher in variable and complex environments than in stable habitats; hence the payoff of exploration should be higher in the former. We would also predict that permanent or seasonally resident species should explore their areas more than species that stay in one location for only short periods. Resident birds must cope with seasonal changes, and continuous exploration helps them do so. In contrast, truly nomadic or facultatively migratory species may leave an area if conditions worsen, and detailed information on local conditions will have less long-term value (Mettke-Hofmann, 2000a).

1.4. Costs and Benefits within Two-Factor Models of Exploration and Neophobia

The foregoing considerations of costs and benefits are based on the assumption that neophilia and neophobia are different and opposite responses along a single behavioral continuum. In this view, an animal in the presence of a novel object may be motivated by fear or, alternatively, by curiosity and will behave (retreat or approach) accordingly. The independent variable is the degree of novelty that the object or situation has for the animal, whose motivation and behavior vary accordingly. At low levels of novelty, it experiences little physiological excitement and may approach the object or ignore it altogether. With increasing novelty, curiosity and motivation to explore reach the point at which they shift to fear and, consequently, withdrawal; at the transition from the one motivation to the other, vacillation will cause the animal tentatively to approach and withdraw, with varying degrees of ambivalence (Hughes, 1997; Hogan, 1965; Thorpe, 1956).

In contrast to the single-factor model, a predominant psychological view (Russell, 1973) holds that neophobia and neophilia are associated with two distinct yet related systems. The single- and the two-factor

models may often predict a similar pattern of behavior, but the dynamics of the predicted responses will be different. For example, animals often engage in low or zero levels of exploration of highly unusual objects. The single-factor explanation is that neophobia is the response to that level of novelty. In contrast, the two-factor model supposes the underlying mechanism is that neophobia and neophilia are aroused simultaneously, but that neophobia inhibits a neophilic response when the levels of novelty are high (Hughes, 1997; Russell, 1973; Chance and Meade, 1955; Montgomery, 1955). That is, increasing novelty might generate a linear intensification of neophobia, but the increase in neophilia might be less steep or might reach an asymptote while neophobia continues to rise.

The two-factor model is analogous to the process of driving a car and employing both feet—one on the accelerator and one on the brake pedal. Ordinarily, the braking and accelerating systems are coordinated: When one system is in action the other is not. However, both systems may be in action simultaneously, with one counteracting the other and causing a highly ambivalent response. Such decoupling of neophilia and neophobia has received little theoretical work or experimentation. As we will discuss further, the difference in the two models becomes particularly important if the levels of the neophobia and neophilia respond differently to ameliorating factors, particularly to habituation. Furthermore, with regard to the evolution of novelty responses, selection can act independently on the two physiological systems and thereby produce a more complex array of behavioral phenotypes.

In a cost–benefit analysis, the exploratory tendency will be more sensitive to selection from the benefits curve than from the cost curve. Exploration (neophilia) will increase under circumstances in which information about new resources will yield the greatest benefit, i.e., circumstances of habitat complexity, hidden food sources, and unpredictable and variable resources. In contrast, we hypothesize that neophobia will be more sensitive to the cost function, increasing in more dangerous environments or those in which interspecific competition is greater. Based on these considerations, we have devised a two-by-two matrix that makes simple predictions regarding the intensity of responses under different cost/benefit regimes (Figure 1). This simplified analysis indicates that where costs of exploration are low and benefits high (as might be true on an island), we expect high exploratory and low neophobic tendencies and where the cost of approaching a new object is high and the benefits low (as in a mainland tropical forest), we expect high neophobia and low exploration. These two sets of conditions would establish the end points of a continuum of novelty re-
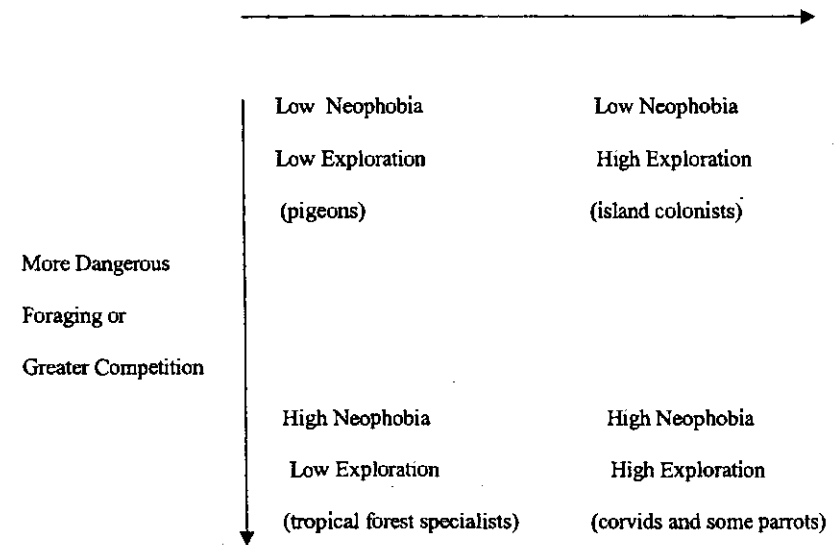

FIGURE 1. Simple two-by-two matrix (see Section 1.4) demonstrating the occurrence of neophilic exploration and neophobia in response to general environmental variables.

sponses that would also be predicted by a single factor mechanism (i.e., neophobia gradually diminishes and transforms into neophilia, which in similar fashion can gradually increase). However, where the potential benefits and the potential dangers of approaching a new situation are both high, the behavioral solution is to apply the brakes and the accelerator at the same time; therefore, the bird approaches the new object with a high degree of ambivalence. This model provides, we believe, a reasonable description of the novelty responses of ecologically plastic, yet wary birds such as corvids (and it explains why such birds are so hard to trap).

2. HOW NEOPHOBIA AND NEOPHILIA ARE STUDIED

2.1. Assessing Neophobia and Neophilia

Neophilia and neophobia have been tested under different experimental paradigms and, as we have stated, in theory they probably reflect motivationally independent responses. Neophobia is often presented as

a simple preference for familiar food and consequent avoidance of novel foods (see recent work on food neophobia in humans, Raudensush and Frank, 1999, for example). But we believe that the distinction between a simple preference for the familiar and an active fear of the novel is an important one. We therefore argue that preference tests in the lab (Rabinowitch 1969, 1968) and in the wild (Marples et al., 1998), while instructive, do not tell the whole story. Studies of diet selection that have documented preference for the familiar often include subjective descriptions of the fear birds show towards new foods (Beissinger et al., 1994; Heinrich, 1988; Coppinger, 1969; Hogan, 1965). We will argue later in this chapter that it may be the intensity of this fear response that differs between more or less neophobic animals.

The intensity of the avoidance response is often tested with novel food, food containers, or objects placed near food. The last two kinds of objects are preferable for studying neophobia because it is difficult to distinguish whether a novel food is ignored because of aversion to the novelty of appearance, or because color or shape render it unidentifiable as food. Cowan and Barnett (1975) and Mitchell (1976) quantified neophobia by placing a familiar food conspicuously in an unfamiliar container and measuring the latency to feed compared to the latency when the container was familiar. Similarly, Greenberg (1983) examined the effect of microhabitat novelty in wood-warblers by measuring latency and number of unsuccessful approaches to feed when novel objects were placed near a familiar cup filled with a preferred food. In this and other experiments measuring latency, controls included absence of novel objects, use of objects that had become familiar in sites other than the food cup, as well as use of objects to which the birds had been familiarized at the food cup (Greenberg, 1990b). Although avian experiments have generally used feeding latency as the primary variable, physiological measures of acute stress also have been taken, such as heart rate or circulating corticosteroid level (Glück and Leisler, 1994; for primates, see Clarke et al., 1988).

In studies of neophilia, objects are presented without food so that their intrinsic attractiveness can be measured (Mayeaux and Mason, 1998; Negro et al., 1996; Heinrich, 1995; Verbeek et al., 1994; Wood-Gush et al., 1990; Raach and Leisler, 1989; Renner, 1987). Behaviors measured include latency to approach and manipulate the objects, as well as duration and frequency of investigation.

2.2. Teasing apart Neophobia, Hunger, and Neophilia

Because neophilia and neophobia may occur simultaneously under the two-factor hypothesis, it is difficult to tease apart their relative

contribution to a particular response. By introducing an additional strong attractant (food for a hungry bird), the neophobia experiments attempted to cut this Gordian knot. To a bird first deprived of food and then presented with it while a novel object is present, the effect of any attraction the object might have had for exploration is overcome by the bird's motivation to eat. We therefore assume that the latency to feed largely reflects the point at which hunger overcomes neophobia and that neophilic exploration is a relatively insignificant source of motivation for approaching the novel object. In this way, feeding latency, when food deprivation has been controlled, permits an estimate of the relative intensity of neophobia.

This assumption that, in comparison to hunger, neophilia provides weak motivation to approach has been challenged. An overriding drive to explore novelty has been suggested as outcompeting other motivational forces and thus becoming the underlying reason for the increased latency to feed at novel objects or foods (Chance and Meade, 1955). This hypothesis was explicitly addressed by Greenberg (1984b). He presented subjects with the same series of objects in the presence and the absence of food reward and determined that the latency to feed at an object was completely unrelated to the initial visitation rate to explore that object in the absence of food (Figure 2). This is the only study that examines exploration and feeding neophobia at the same objects and by the same birds. Mettke (1993), however, examined exploratory tendencies and feeding neophobia of the same birds at different test objects and also found no correlation between the two behavioral measures.

The measurement of "pure" neophilia is more problematic. The presentation of an object without food will engender responses that are the outcome simply of the interaction of exploration and neophobia. For example, a bird that seems to ignore an object in its cage may do so because the object elicits little motivation to explore (neither neophobia or neophilia, i.e., lack of interest) or because any exploratory tendencies that it elicits are inhibited by the fear and avoidance it stimulates. In the future, these two alternatives inherent to the two-factor theory of novelty responses, which we might term indifference versus aversion, may be distinguishable by physiological measures. Such measures include plasma corticosteroid level, heart rate, or patterns of brain activity. These should determine when birds appear to be ignoring an object but at the same time show physiological signs of excitement.

2.3. The Nature of Novel Stimuli

How we determine what is novel and how we estimate the degree of novelty have been problems from the dawn of novelty studies (Berlyne,
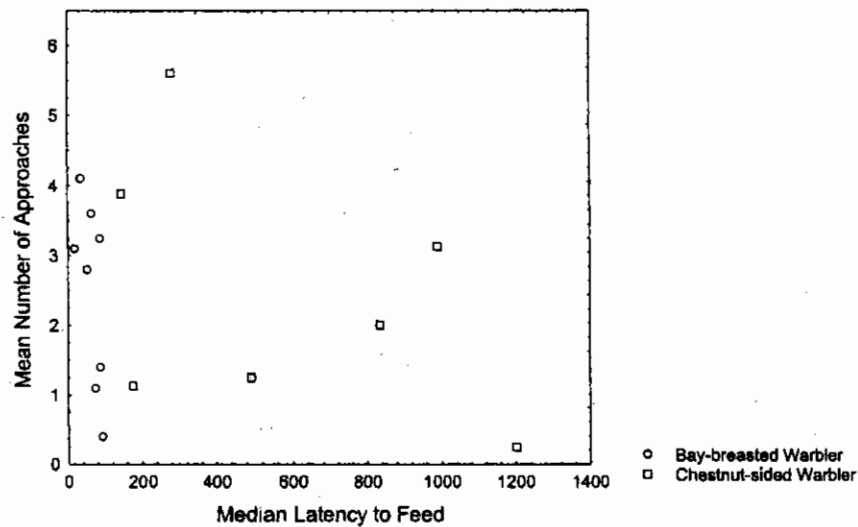
FIGURE 2. Exploration versus neophobia measured in the same individuals of two species of *Dendroica* wood-warblers. Madian latency to faad in the prasance of noval objects is plotted against mean number of approaches to tha sama objects when food attractant is absent (based on Greenberg, 1984b).

1950). For birds reared in a controlled captive environment, the universe of what is experienced is known, and the novelty of an object can be assured (although problems of similarity among objects and stimulus generalization still occur). However, such thorough control of a bird's environment usually renders the environment impoverished in stimuli, which may itself affect overall responses in unpredictable ways. Wild-caught birds, on the other hand, have experienced environments about which we can make only educated guesses. One approach is to select a range of objects that are dissimilar to anything that could be experienced in the wild. A consistent response over a range of such objects makes reactions more confidently attributable to some emergent property (novelty) rather than to reaction to a specific set of stimuli (Greenberg, 1983).

Novelty experiments vary considerably in the specific stimulus or object used to test the response. To the skeptical, measuring response to a single example or series of highly unnatural objects, such as plastic Easter grass or colorful beads, etc.—the *modus operandi* of many novelty experiments—may seem antithetical to gaining an understanding of adaptations that have been shaped in the natural world. However, novelty is an emergent property of any object, natural or otherwise.

Therefore, if a generalized novelty response exists (and the literature supporting this concept is both large and venerable; Corey, 1977), then natural versus unnatural becomes a meaningless distinction. The goal of experiments is to assess the generalized response to novelty, as distinguished from the many potential specific responses to particular stimulus features. Accordingly, it may be necessary to use a range of unfamiliar objects and test for a consistent response, regardless of specific stimulus features. This is more easily done when the range of objects includes the artificial. Most experiments on novelty responses may be flawed because they assess the response to a single object or food type, rather than to a series of novel or potentially novel objects or foods. Nevertheless, experiments that rely upon the presentation of a single object may often assess novelty responses accurately. The reason is that even when a series is presented, i.e., when there is quantitative variation, it is demonstrable that the qualitative reaction to novelty is generally consistent and distinguishable from reactions to the familiar.

2.4. Among Object Variation in Novelty Responses

Novel objects engender wide variation in the intensity of exploratory or neophobic responses. Variation can seem to be idiosyncratic (Greenberg, 1983, 1984b), or it can follow consistent patterns (Heinrich *et al.*, 1995), with certain types of objects stimulating greater fear or exploration than others. Heinrich *et al.* (1995) found a great deal of variation in the speed at which ravens approach and feed at different novel objects, with latencies ranging from less than 1 minute to 16 hours. For example, ravens showed little hesitation to approach small round objects, but extremely large latencies for long, thin objects and for big objects (particularly mammal carcasses). Stimulus intensity and complexity probably have the greatest salience for neophobia (Berlyne, 1950). Thus, if a certain hue is novel and engenders a distinct novelty response, a brighter sample of that hue will stimulate a more intense response (similar arguments can be made for size, shape, complexity etc.). Franchina *et al.* (1994) reared chickens under identical conditions and at days 3, 5, and 7 of life offered them clear water and water that was colored with different intensities of red food color. The more intense the color, the longer the young chickens hesitated to drink. Greenberg (1983) found a tendency for birds to be more neophobic in the presence of brighter colors, larger objects, objects with spines, and objects with more complex surface structure.

Complexity may be the most important stimulus dimension for exploratory behavior; complex stimuli have long been known to sustain

exploration for longer periods (Thorpe, 1956; Berlyne, 1950). For example, Jones et al. (1996) presented chickens from their first day of life onward either with a blank but illuminated computer monitor or a monitor having a complex screensaver. At day 9 both images were presented in a two-choice runway with one image or the other at each end. Birds familiar with the complex screensaver significantly preferred this image, while birds familiar with the simple image showed no preference for either image.

Finally, novelty may be dependent upon the context of the stimulus. It is well established in the psychological literature that a novel object in a familiar setting will elicit a more intense response than that same object in a novel setting (Cowan, 1976). This presumably relates to the discrepancy between the stimulus and its setting (the "surprising" aspect of novelty). Furthermore, a familiar object in a novel setting may be treated as itself novel, or a novel object may elicit an enhanced novelty response if it incorporates stimulus features that have been uncommon in the bird's rearing environment. To express the latter two distinctions, we coin the terms *situation-specific novelty* versus *general novelty*. The former refers to the novelty of an object when compared to the whole class of objects to which it belongs (e.g., a food item with a color pattern distinct from colors previously experienced by the bird in its diet on that same item) and the latter signifies the novelty of an object is based on features that distinguish it from what a bird has generally experienced before (e.g., a bright and unusual color).

2.5. Innate Bias in Novelty Responses

Some of the variation in the avoidance response to novel objects may be determined by innate individual predispositions to particular stimulus features. Avoidance may disappear with repeated exposure, so that the ultimate role of familiarization with a novel stimulus is to reduce the variance attributable to original innate biases. The prime examples of innate bias are initial responses to aposematic patterns associated with dangerous prey, from colors generally that are warning (Mappes and Alatalo, 1997; Schuler and Roper, 1992; Schuler and Hesse, 1985; Schuler, 1982) to specific patterns of venomous snakes (Caldwell and Rubinoff, 1983; Smith, 1975).

Experiments demonstrating an innate predisposition to avoid a particular stimulus can be difficult to interpret, however, unless the distinction is made and controlled for between situation-specific and generalized novelty. For example, the avoidance response is often stronger for brightly colored than for dull-colored foods (however, see Marples et

al., 1998); this result has held true for the pioneering studies of gull diet by Rabinowitch (1968) as well as for more recent studies of insect selection (Schuler and Hesse, 1985) and seed selection (Mastota and Mench, 1994). Response to bright coloration might be innate, selected for by a frequent association between bright colors and distasteful or poisonous food. However, it is likely that the general rearing environment of a predator will have fewer bright colors, with the result that a dull-colored prey item is less novel to a naïve individual. To test this, Roper (1990) conducted an experiment with chicks, controlling both prey color and rearing-environment color, and was able still to demonstrate an innate bias against bright red prey.
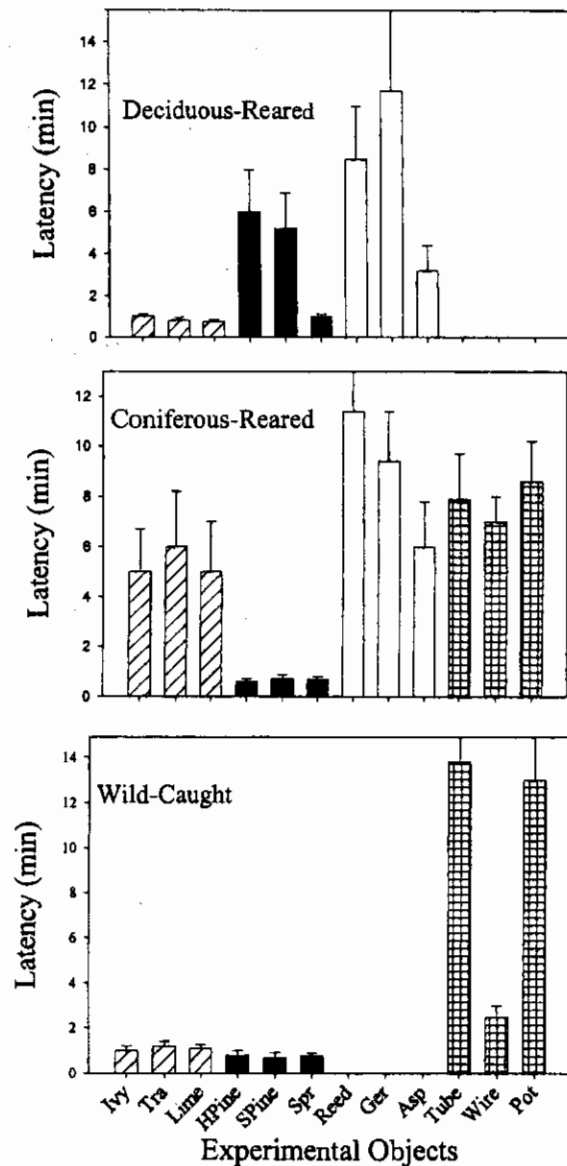
Variation in responses to comparably novel stimuli is not restricted to potentially dangerous prey. Grünberger and Leisler (1993) raised Coal Tits under four conditions: (1) artificial coniferous foliage, (2) deciduous foliage, (3) enriched habitat; or (4) depauperate artificial non-plant habitats (Figure 3). Feeding neophobia was tested by measuring the latency to feed at familiar or novel foliage (three types of plants or other objects from each rearing condition plus three deciduous plants novel to all treatment groups). All groups showed significantly shorter latency to feed at the familiar than at the novel foliage. Surprisingly, the group whose experience was with deciduous foliage reacted with similarly low latency to spruce foliage but not to the unfamiliar deciduous foliage (Grünberger and Leisler, 1990). Coal Tits are coniferous specialists and are especially fond of spruce. The low neophobia that individuals displayed when in the presence of spruce foliage was interpreted as part of an innate predisposition to species-typical coniferous habitat.

3. WHAT DETERMINES THE INTENSITY OF NEOPHOBIA AND NEOPHILIA IN ADULT BIRDS?

3.1. The Process of Familiarization

The response to any particular object or prey item will result, in part, from the interaction of an intrinsic novelty response and whatever familiarity the bird has with the same or a similar object. This section will first address the dynamics of how the transition from novel to familiar might occur and then discuss factors that determine the intrinsic response to novelty.

That a response to an unfamiliar object has a significant component of neophobia implies that the aversion will be reduced or eliminated by familiarization, i.e., by habituation. The pattern and tempo of such

FIGURE 3. Influence of rearing conditions end innete preferences on neophobia of young Coal Tits (*Parus ater*). Bars show mean latency (± 1 SE) to feed at 12 different experimental objects by individuels reared in either artificial deciduous habitet (top penel), individuals reared in artificial coniferous habitat (middle panel), or wild-caught individuals (bottom panel). Hatched bars: artificial deciduous structures; black bars: artificiel coniferous structures; white bars: other artificial plant structures; checked bars: artificial non-plant structures. Treetment groups represented in top and bottom panels were exposed to three types of experimental objects. Experimentel objects (and their abbreviations, when abbreviated) were Ivy (*Hedera* sp.), *Tradescantia* sp. (Tre), lime (*Tilia* sp.), hard pine *Pinus* sp. (H Pine), soft pine (S Pine), Spruce *Picea* sp. (Spr), reed (*Phragmites* sp.), *Geranimum* sp. (Ger), *Asplenium* sp. (Asp), tube, wire, flowerpot. [Reproduced from Grünberger and Leisler, 1993, with permission from *Journal für Ornithologie*).

habituation has rarely been explored in captivity and never been measured, as far as we know, in the field. Captive studies consistently show that after the first handling of, or feeding on or at, a new food or feeding site, performance rapidly approaches that for familiar sites or foods. Heinrich et ol. (1995) presented curves of the latency with which Common Ravens made contact with new foods when presentations were repeated (Figure 4); these show similar patterns of habituation irrespective of the original degree of aversion. Greenberg (1990a) presented similar graphs for repeatedly presented novel feeding microhabitats. He selected from a group of Swamp Sparrows (*Melospizo georgiono*), whose initial latencies were greatest and continued to present the novel microhabitats until feeding occurred within 20 minutes. Although it took up to five days of trials for the first feeding to occur, subsequent feeding latencies were similar to those of the controls (individuals feeding at a familiar cup), and they remained low.

Repeated exposure to an object reduces exploration as well as avoidance. A decrease in the number of contacts with the object during repeated presentations has been demonstrated in several studies of birds (Heinrich, 1995) and mammals (Renner and Seltzer, 1991; Poucet et ol., 1988; Welker, 1956). On the first day of presentation, the preference of Common Ravens for both novel edible and inedible items (measured in the number of approaches) was hundreds to thousands of times greater than for such items as twigs, seeds, bark, which were a familiar part of the background in the aviary; the birds nearly ignored the inedible items after two days (Heinrich, 1995).

As in most feeding tasks in which there is habituation to an object, after the object has not been encountered again for a period of time, latency to feed may rebound to high levels (Thorpe, 1956). This phenomenon of "spontaneous recovery" was investigated for microhabitat neophobia in mature wood-warblers (Greenberg, unpublished). After
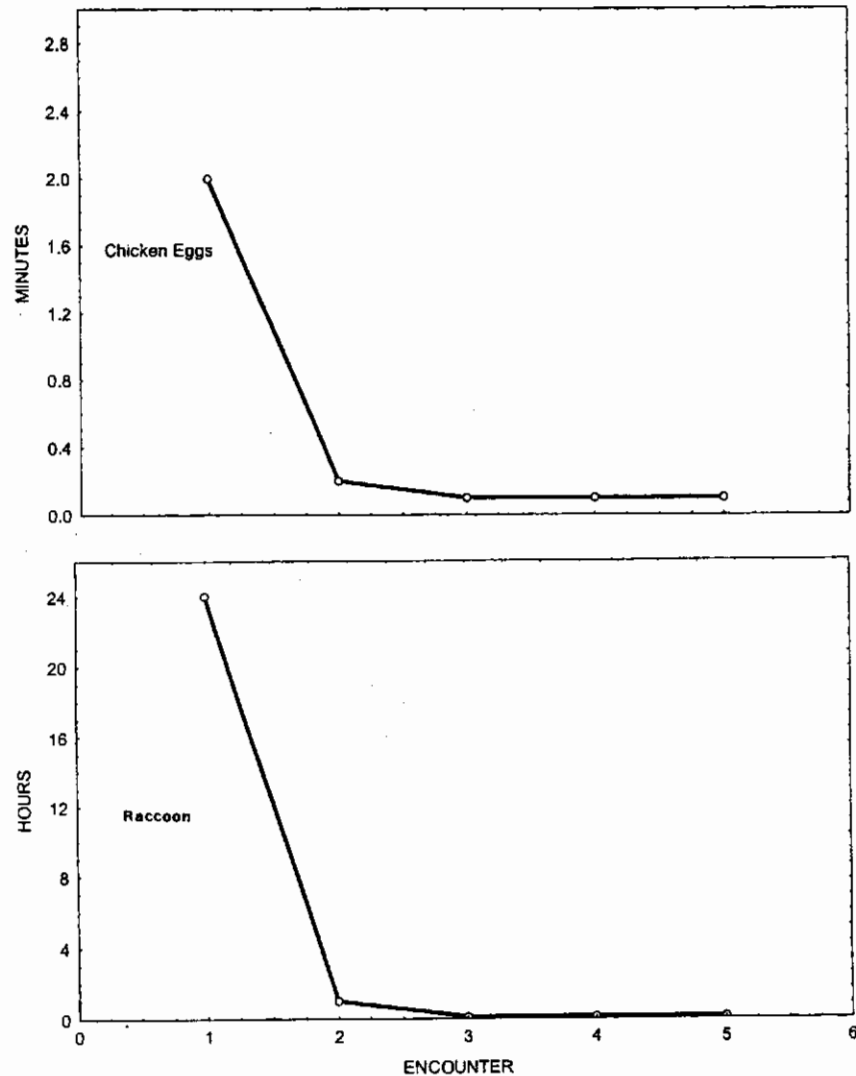
FIGURE 4. Change in latency to feed during repeated presentations of two novel foods (chicken egg and raccoon [*Procyon lotor*] carcass) to one group of three Common Ravens (*Corvus corax*) (based on Heinrich *et al.*, 1995, with permission from the American Ornithologists' Union).

latency of individuals to feed at a food cup near an object had decreased to that of the control group (food cup, no object), removal of the experimental object for one week caused a substantial recovery of the original latency; after removal for four weeks, latency was indistinguishable from that of the first exposure. This suggests that, at least for mature birds, some continued exposure may be necessary to maintain familiarity. It further suggests that memory of familiar objects may be relatively short and that continued exploration is required to maintain an object's status.

3.2. The Dynamics of Exploration and Neophobia

Familiarization can result from forced exposure to an object, as in many of the experiments mentioned. In nature, however, novel objects may simply be bypassed and therefore remain novel. How familiarization would occur in the wild, where birds presumably are free to avoid the fear-provoking stimulus, is a central paradox of the role of novelty.

Heinrich (1988) reported that although ravens often approach new foods, they do so with a stereotypic response that appears to be the result of simultaneous attraction and fear. Ravens first land ten or more meters from the food, then approach it; as they near it they often perform a leaping maneuver, and their final approach consists of jumping on, then fleeing, the food. This ambivalent response had been noted decades earlier by Lorenz (1956: 35):

> A young raven, confronted with a new object, which may be a camera, an old bottle, a stuffed polecat or anything else, first reacts with escape responses. He will fly up to an elevated perch and, from this point of vantage, stare at the object literally for hours. After this, he will begin to approach the object very gradually, maintaining all the while a maximum of caution, and the expressive attitude of intense fear. He will cover the last distance from the object hopping sideways with half-raised wings, in the utmost readiness to flee. At last, he will deliver a single fearful blow with his powerful beak at the object and forthwith fly back to his safe perch. If nothing happens he will repeat the same procedure in much quicker sequences and with more confidence.

In the dance of the raven we see the dynamic nature of novelty responses. Ambivalence suggests that two systems are operating, which may solve the conundrum of neophobia: How do birds habituate to novel objects if their main response is one of avoidance? In many birds, the motivation to explore can occur simultaneously with the aversion to novelty. The relationship between a bird and its environment is, to a great degree, under the control of the bird and is not simply the result of passive responses to exposure to a particular set of objects. Mobile

animals actively select their environment and determine what is familiar by the way they explore it. For a bird to show ecological plasticity as an adult and to discover new resources, reduced neophobia must be coupled with a greater exploratory tendency or responsiveness to social facilitation.

The temporal dynamics of the habituation that occurs during neophilia and simultaneous neophobia in the two-factor model has not been well studied. Hogan (1965) showed a relatively tight temporal coupling between changes in approach and withdrawal tendencies in chicks facing their first mealworms and suggested that this coupling is evidence that the approach and withdrawal responses are the results of a single system. If two different systems, rather than one, account for exploration and avoidance, then these two are well integrated. However, the possible decoupling of the rates of neophobia and neophilia during habituation is suggested by experiments of Mettke-Hofmann (2000a). For two days, she introduced three novel objects into the familiar aviary of six species of Loriini and four species of Platycercini (Psittacidae). Conspecifics were held in dyads. In each dyad, the first bird that made contact with the objects exhibited similar latencies on each day. However, the second bird in each dyad that made contact did so significantly more quickly on the second day. Some familiarity with the objects achieved during the first day of presentation coupled with a slower reduction in neophilia might have caused the shorter latencies in the second birds.

Habituation to novel objects also includes qualitative changes in behavior. For nonhuman primates, Todt et al. (1992) described three phases for the engagement with objects: First, objects are visually, orally, or tactilely explored; second, they are handled or carried in a playful manner; and third, they are used in a social context. The degree to which these three phases can be found in birds has not been formally tested and will presumably vary with age, social relations, and species-specific ecology. In parrots Mettke (unpublished) was able to document behavioral changes that began with cautious inspection of an object using only the bill, followed by more intensive manipulations using the feet and bill.

Some animals may confront novelty not simply as the result of chance but may actually seek it out—the "inquisitive exploration" of Birke and Archer (1983). This is an extremely difficult proposition to investigate, but Wood-Gush et ol. (1990) developed a clever approach to the problem by offering piglets (Sus scrofo) two side pens adjacent to the home pen, each side containing either a hidden novel object or a familiar object. The pen containing the new object was indicated by various cues, e.g., a Danish flag. The piglets preferred the pen containing the hidden novel objects, suggesting that they were seeking novel situations. The facts that throughout the experiment the piglets spent more time in the pen with novel objects, even when they visited the familiar pen first, and that there was a learning curve for making the initial choice of the novel pen, argue against their being attracted by other cues. No comparable studies are available for birds.

3.3. Social Facilitation and Novelty Responses

Birds often do not encounter novelty when they are alone. Participating in flocks and responding to the approach behavior of other individuals may play a critical role in allowing individuals to overcome neophobia. Galef (1993) hypothesized, and Visalberghi and Fragaszy (1995) later showed for a capuchin (Cebus) monkey, that social facilitation has a greater influence on the consumption of novel foods than on consumption of familiar foods. Visalberghi et al. (1998) went on to demonstrate that social facilitation speeds up the familiarization process that in individuals otherwise occurs more slowly.

Exactly why, and under what circumstances, social interaction should catalyze responses to novel objects has not been formally addressed. There is considerable room for developing predictive hypotheses concerning the effect that potential benefits, which may vary interspecifically, may have on flock members' responses to novelty. Here we develop two sets of hypotheses; these differ in whether substantial asymmetries in dominance or experience exist in the social groups.

3.3.1. Asymmetrical Payoff Hypotheses

3.3.1o. Differential-Experience Hypothesis: In groups of birds whose members differ in experience with the novel object or food, experienced birds will display reduced neophobia, thus signaling to the others that there are no negative consequences of approaching the novelty. To extend this idea, the individual differences in experience can be derived during the initial encounter, as the result of individual variation in intrinsic neophobia. The result will be that the response of the entire flock, while it varies according to individual, tends to converge upon that of the least neophobic individual.

3.3.1b. Differentiol-Dominonce Hypothesis: Regardless of equality of experience, the potential payoff that dominants gain from approaching novel objects is smaller than the payoff of subordinates be-

cause dominants, having freer access to limiting resources, are in lesser need; therefore, mid- or even low-ranking individuals in a group's dominance hierarchy should take greater risks for resources (Lahti *et al.*, 1997; Hegner, 1985). Dominants may observe subordinates as a way of testing for the safety and usefulness of a new resource (e.g., producers versus scroungers; Drent and Marchetti, 1999; Wilson *et al.*, 1994), and the resulting social facilitation tends toward the convergence of the behavior of members of the hierarchy.

3.3.2. Symmetrical Hypotheses

3.3.2a. Group-Protection Hypothesis: In groups with homogeneous experience and no established dominance asymmetries, the simple presence of other birds provides potential reduction of any negative consequences of approaching a novel object or food item. This type of social situation may be common in birds in large flocks unstable in composition. Because the group may deter predation but cannot minimize the effect of ingesting toxins, under this hypothesis we would expect social facilitation to be more prevalent in novelty response to objects or space. Social facilitation in diet selection should occur only in groups whose members have mixed experience.

3.3.2b. Competition Hypothesis: The presence of other individuals, all of the same status, increases the cost of hesitating to explore a potentially useful resource.

Patterns in approach latency may allow us to distinguish which of the above hypotheses best explains how flock participation affects responses to novelty. Under the asymmetrical hypotheses, we would expect the latencies of individuals in groups to converge upon, but not be less than, the solitary performance of the experienced or subordinate individuals. Further support for the differential-experience hypothesis would come from finding differences in group mean latencies between groups that do and groups that do not contain individuals experienced with a novel object. The differential-dominance hypothesis would gain support if there were correlations of group latencies with an independently derived measure of dominance. For the symmetrical hypotheses, we would expect low interindividual variance in response coupled with a minimum individual latency that is less than the lowest latency found in tests of solitary individuals.

Because these hypotheses for the possible roles of social facilitation have not heretofore been formalized, there have been no true tests. However, we can provide examples from experiments on social facilitation

and novelty that seem to be consistent with the different hypotheses. For example, the results of the study of Coleman and Mellgren (1994) on social feeding's effect on neophobia in Zebra Finches seem most consistent with hypothesis A-1 (Asymmetrical Payoff-Differential Experience). Trials consisted of presenting novel feeders (a box or a cylinder, which birds had to enter) or novel objects (one of four unusual objects placed inside the feeder next to the food). For each set-up, half the birds were tested in groups of three and the other half as solitary individuals. Tests were presented in two phases: Solitary birds were subsequently tested as flock birds, and vice versa. The results were that the average latency to feed at the novel feeders and the feeders with novel objects were significantly lower for the birds feeding in groups. The effect, however, was to reduce the latency of the second and third bird rather than the latency of the first bird. This result was based purely on a following response, since group members could see the pioneering individual as it went to the novel feeder, but could not observe it as it fed.

Greenberg (1987a) examined hypothesis A-1 as it applied to the interspecific flocking of the specialized and highly neophobic Chestnut-sided Warbler (*Dendroica pensylvanica*) caged with the generalist and non-neophobic Bay-breasted Warbler (*D. castanea*). He presented novel foraging sites to Chestnut-sided Warblers when alone and in the presence of a pretrained Bay-breasted Warbler. The availability of multiple feeding sites minimized the importance of direct dominance interactions. There was no evidence that the neophobia of the Chestnut-sided Warbler was at all reduced in the presence of the trainer. This experiment raised the issue of appropriate behavioral models in heterospecific groups. Greenberg argued that the Chestnut-sided Warbler on its tropical wintering grounds characteristically occurs in mixed-species flocks, but as the only member of its species in the flock. As a specialist, it is unlikely to respond to the behavior of heterospecifics with different foraging patterns.

So far, despite increased interest in characterizing variation in temperament among individuals of social groups, studies examining the relationship between neophobia and dominance (Asymmetrical Payoff-Differential Dominance, hypothesis A-2) have been few and inconsistent in results. Katzir (1983, 1982) considered the latency of feeding on a novel food (roaches) and exploration of new space by captive-reared Jackdaws. By scoring the winner of dyadic agonistic interactions at food, he independently assessed dominance within each of three social groups. He found that an individual "initiator" Jackdaw of mid to low rank fed on the novel food more promptly than did a dominant Jackdaw. Heinrich *et al.* (1995) examined neophobia (as estimated by latency to

feed at unfamiliar bait) as it related to dominance in three groups of captive-reared Common Ravens. In this study, alpha dominant birds fed more rapidly at novel objects when foraging latencies were not great, but for truly aversive novel objects mid-ranking birds made the first feeding visits.

In contrast to the foregoing, several investigations reported that dominant individuals in their familiar environment explored novel objects as much as or more than did subdominant members. Dominant and subdominant parrots were equally likely to be the first to feed when a known object (an additional feeding dish) or an unknown object (a cotton mop) was placed beside the feeding dish (Mettke, 1993). In a related experiment (Mettke-Hofmann, 2000a) focusing on neophilic exploration, dyads in familiar aviaries were simultaneously offered three objects, and there was no relationship between a member's rank and first tactile contact with the novel object. Duller, less conspicuous plumage was actually a better predictor of which bird in a dyad would first explore the object. Perhaps more visually cryptic individuals incur less risk of a surprise attack in an unfamiliar situation.

In 1-year-old Keas (*Nestor notabilis*) tested in a group, dominant birds explored a novel object longer than did subdominant birds (Kubat, 1992). Similarly, in 19 of 22 parrot species the dominant bird made contact with a new object sooner and explored it for a longer time than did the subdominant members of the group (Mettke, 1995). Finally, dominant domestic hens explored more than did subdominant ones, even when tested separately (Wünschmann, 1963).

This variation in results of studies relating dominance and novelty responses should not be surprising, if the individual birds assess the expected payoff of exploration. After all, the inherent danger of exploration and the likely benefit of the information to be gained will vary according to the habitats and foraging strategies of the species involved. The problems of approaching novel situations by birds in flocks is an area ripe for the development of predictive models. Such models should incorporate the probability of harm resulting from approaching the novelty, the potential benefits, and the probability of capitalizing on the benefits as a function of social rank. From an empirical point of view, greater care should be taken to measure both neophobia and dominance independently of their interaction effects.

Two studies of large groups of naïve young birds suggest the importance of the two symmetrical hypotheses (B-1, B-2). Immature Common Ravens often occur in flocks when individuals feed together outside the established territories of adults. Marzluff and Heinrich (1991) presented experimental evidence that this flocking reduces average and minimum
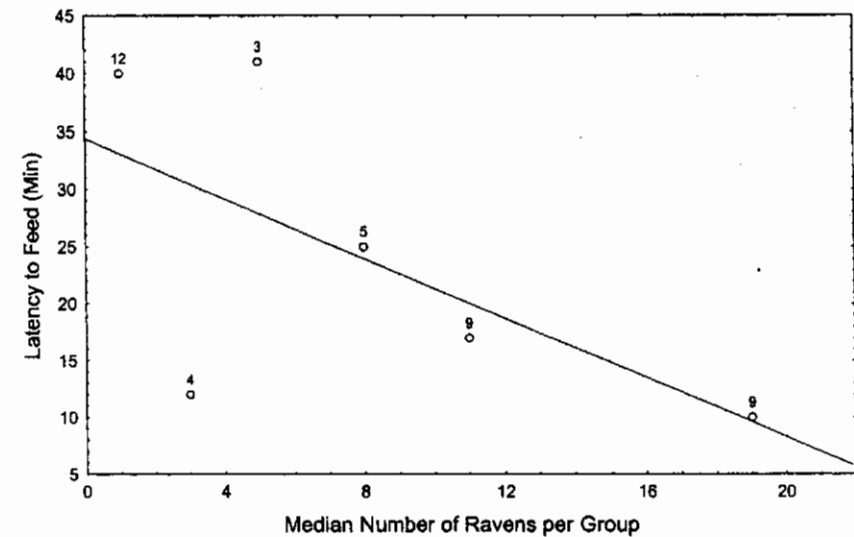

FIGURE 5. Latency of Common Ravens (*Corvus corax*) to feed at a novel object, plotted against median group size for five classes of group-size (based on Marzluff and Heinrich, 1991, with permission from Academic Press).

neophobia, measured by both latency to feed and number of approaches prior to feeding; both measures decline with group size (Figure 5). In addition, preliminary results of Bolan and Greenberg (unpublished) suggest that latencies owing to object neophobia are generally lower and much less variable in immature American Black Ducks (*Anas rubripes*) when tested in groups than when tested individually; all ducks in groups fed faster, on the average, than the fastest duck when tested solitarily.

3.4. Consistent Individual Variation in Neophobia

Although usually not an explicit focus of the neophobia studies reviewed thus far, individual variation is often substantial. In most of these studies, only one or a few objects or foods were presented to an individual, so it is not possible to assess consistency. However, in both Wood-warblers (Greenberg, 1984b, 1983) and sparrows (Greenberg, 1989) to which a number of novel objects were presented, individuals showed a statistically significant consistency in rank of latencies, suggesting the existence of more and of less neophobic individuals.

3.5. Genetic Basis for Intraspecific Variation

The primary evidence for a quantitative genetic basis for different levels of neophobia is the variation found between the performance of different strains (often domestic versus wild type) of rats, chickens, and mallards reared under identical laboratory conditions (Murphy, 1977; Mitchell, 1976; Cowan and Barnett, 1975; DesForges and Wood-Gush, 1975). In general, domestic strains are less reactive than wild types, presumably owing to selective breeding for animals adaptable to conditions of captivity. In one of the few selection experiments, Drent (1997) used four generations of Great Tits (*Parus major*) to select for divergent lines of fast- and slow-exploring birds. Individuals were labeled as "fast and superficial" or "slow and thorough" on the basis of three measurements of exploration, which were all strongly correlated (see Verbeek *et al.*, 1996). Fast and superficial explorers that approached novel objects more promptly in their familiar environment also took less time to reach the destination in a novel environment and spent less time exploring than birds that approached novel objects more slowly (slow and thorough explorers). A combined test score was obtained from the sum of linear conversions to a 0–10 scale. The scores for the fast selection line increased linearly from generation F1 to F4, whereas scores for the slow selection line decreased linearly (Figure 6), resulting in an estimated heritability of 52%. The finding of heritable variation for the combined performance on different exploratory tasks dovetails nicely with the recent focus on the evolution of temperament. However, the specific controlling behavioral trait that underlies the variation in performance remains unclear.

Marples and Brakefield (1995) were able to select Common Quail for two divergent lines that incorporated a "semi-palatable" and novel prey into their diet; one line did so at a fast rate, one at a slow rate, and the reselection occurred over only three generations. The authors attributed the underlying difference to a response to novel food items. However, the two lines did not respond differently to novel nonfood objects placed into their environment, which implies either that novelty associated with diet selection is not associated with a generalized neophobia or that neophobia alone was not the basis of the divergence between strains.

This same study raises the issue of the relationship between object neophobia and other fears. A proposed mechanism associated with bold and timid behaviors is the reactivity of neural networks within the hypothalamic-limbic system (Kagan *et al.*, 1988). Dopamine in the nucleus accumbens septi may be what controls the vigor of either approach
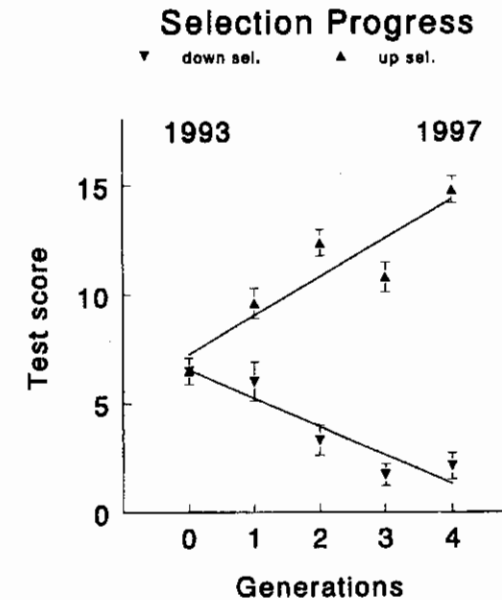
FIGURE 6. Changes in exploratory tendency (see Section 3.5 for explanation of scores) in a four-generation selection experiment on Great Tits (*Parus major*) (Drent, 1997). Mean values of combined score (± 1 SE) on two behavioral tests performed 35 days after hatching, according to generation number. Tests consisted of exploring an unfamiliar environment (test room) and an unfamiliar object in a familiar environment. Selection for higher (up) and lower (down) exploration tendency (speed) were started from a common base population collected in the field (Drent, 1997).

to or withdrawal from novelty (Ikemoto and Panksepp, 1999). Because of the existence of systems that appear to control the intensity of responses to a variety of stimuli, this reactivity could be a response in a number of different contexts, rather than being "domain specific" (Wilson *et al.*, 1994). The idea that there is a generally fearful behavioral phenotype in mammals and birds that transcends narrow and particular contexts is receiving renewed support (Boisy, 1995). The concept is also consistent with the apparent ease with which some domesticated species have shown reduction in fear responses to a variety of situations. Quail from fearful and unfearful lineages (selected on the basis of duration of the tonic immobility response) show differences in the tendency to incorporate novel foods into their diet (Turro-Vincent *et al.*, 1995). Quail that are generally more fearful (and those tested solitarily) tend to eschew novel foods more completely than do less fearful individuals.

However, not all studies have supported the idea that neophobia is related to some general fearfulness. Seferta (1998), for example, argued that the levels of wariness displayed by pigeons and doves feeding in the presence of humans is not necessarily related to neophobia.

3.6. Neurobiological Basis for Novelty Responses

Understanding how selections can act on responses to novelty and how general these responses may be requires deeper understanding of their neurophysiological bases. Variation in fear of novelty in humans and other mammals has been associated with the threshold of excitability of neural circuits of the hypothalamic-limbic system, particularly the amygdala (Kagan et al., 1988). In birds the homologous portions of the archistriatum have been implicated in fear responses (Lowndes and Davies, 1995; Phillips and Youngren, 1986), conditioned avoidance (Lowndes and Davies, 1995), and filial imprinting, which is integrally related to novelty responses (Lowndes et al., 1997). However, the one study measuring responses to novel objects in chicks with archistrial lesions found no decrease in avoidance (Lowndes and Davies, 1995). Turning to neophilia, in mammals reactivity of certain neural receptors to dopamine and other transmitters is related to increased activity in the face of and preference for novel places (Bevins et al., 1999; Beesher et al., 1999; Ikemoto and Panksepp, 1999). Recent work on human behavioral genetics has suggested that the activity of certain dopamine receptors associated with neophilia can be assigned to identifiable loci (Benjamin et al., 1996; Ebstein et al., 1996; but see Sullivan et al., 1998). Similar work has not been done on birds.

3.7. Neophobia and Gender

Perhaps the most obvious potential social correlate of novelty responses is gender. The high testosterone levels of most males can indirectly influence their response to novelty. Testosterone is known to increase persistence of attention to particular stimuli (Andrew, 1972; Andrew and Rogers, 1972). For example, Jones (1986) found that male domesticated chicks were significantly more hesitant than females to feed on novel colored food. He suggested that might be because males attend to the novel color instead of to feeding. Beyond this proximate explanation, we know of no evolutionary hypotheses for gender-related differences in novelty responses. Presumably, such sex-related differences might be related to sex-specific physiological demands and possibly to differential investment in young according to their sex. However, such factors have not been explored, either theoretically or empirically.

3.8. Novelty Responses and the Socioecological Niche

Researchers working on the behavioral ecology of social animals, particularly primates, have argued that novelty responses are part of a constellation of characteristics that make up temperament and collectively affect the performance of animals in a group (Budaev, 1997; Clarke and Boinski, 1995). This argument is conceptually different from the previous discussion of the relationship between novelty responses and dominance, because the variation that it focuses on is an intrinsic feature of the individual bird, presumably has a genetic basis that is maintained, in part, by frequency-dependent selection, and is not simply facultative change that occurs with changing social relations (Wilson et al., 1994).

How a large variation in temperament, if genetically based, can be maintained in a population was explored theoretically by Wilson et al. (1994), who proposed density- and frequency-dependent models based primarily on the concept that varying bold and shy temperaments are adapted to subhabitats that have different levels of relative safety. The authors defined conditions in which individuals that show facultative shifts of temperament would do better than individuals with rigidly determined temperaments. More recently, however, Wilson (1998) argued from an adaptive point of view that the selective pressure causing individual differences in behavior in one context can be different from the pressures acting in other contexts, resulting in domain-specific reactions that might even be expected to be negatively correlated across domains. For example, individual Pumpkinseed Sunfish (Lepomis gibbosus) that are bold in exploring a novel food source are not necessarily bold in another threatening situation (Coleman and Wilson, 1998).

We have covered ways in which novelty responses and dominance might be facultatively related, but the concept of temperament goes beyond this. It asserts that responses to risky situations, whether they are social situations or the presence of a novel feature in a familiar environment, reflect a general intrinsic response to risk. Furthermore, these responses may be relatively stable and result from very early experience or genetic variation. An example is the bold and shy temperamental types found by Kagan et al. (1988) to exist in human infants; type characteristics show at least some consistency in 4-year-old children (Kagan et al., 1998). The intertwining of the novelty response with boldness and shyness in social situations is to be expected, since response to novelty has often been used as an empirical test of temperament in primates (Clarke and Boinski, 1995; Kagan et al., 1988). In fact, novelty responses form an integral part of the accepted definition of temperament for primatologists. Thus Clarke and Boinski (1995: 105)

state: "*Temperament* may be considered a characteristic response style to novel stimuli or challenging situations that is largely independent of immediate or volitional influences...."

To what degree do novelty responses reflect other tendencies toward or away from bold or risk-taking behavior (Drent and Marchetti, 1999; Coleman and Wilson, 1998; Budaev, 1997; Greenberg, 1995)? For birds, the relation between exploratory behavior and intrinsic aggressiveness was explored in a series of experiments on Great Tits (*Parus major*) (Verbeek et al., 1999, 1996, 1994). In pair-wise confrontations, fast and superficial explorers initiated and won more fights than slow and thorough explorers, which the authors attributed to a more active response to stress in the fast-exploring and dominant individuals. The relationship between fast and slow exploration and degree of aggressiveness was tested for groups that contained five to eight Great Tits. In contrast to the results of pair-wise tests, once a stable hierarchy was established, slow explorers had on average a higher dominance score than fast explorers (Verbeek et al., 1999). The latter seem to have found it more difficult to cope with defeat in encounters in aviaries, where escape from social interaction was not possible. Again, what makes the results of this study particularly interesting is that one temperamental characteristic, exploratory behavior, shows a high degree of heritability and is correlated with a second characteristic, dominance. This means either that exploratory behavior directly affects dominance status or that the selective forces on the two aspects of Great Tit behavior are highly correlated.

3.9. Facultative Changes in Novelty Responsiveness

Much of the work on neophobia and exploration has been directed at characterizing "typical" behavior of species or of demographic classes of individuals under comparable conditions. However, we expect that, like most other aspects of learning, behavior toward novelty will show considerable facultative variation in response both to factors internal to the individual (such as hunger and condition) as well as external factors (food distribution, number of competitors, predator abundance, etc.) when internal factors are controlled for. In domestic fowl, some research has investigated changes in neophobia in chicks subjected to increasing levels of food deprivation. Hogan (1965) reported that food deprivation had little effect on the neophobia displayed by chicks in their first encounter with a mealworm. In the only study on wild bird species, Greenberg (unpublished) found that individuals of several species of *Dendroica* Wood-warblers deprived of food for one

hour and for seven hours showed no significant decrease in latency to visit a feeding dish next to a novel object. We know of no study of variation in neophobia or exploratory behavior with variation in overall physiological condition.

Substantial changes in foraging behavior and habitat selection have been found in experiments that varied exposure to potential predators (Lima and Dill, 1990). Given the potential role of risk in shaping novelty responses, facultative changes in such behavior should be tested in experiments that vary the number of encounters with potential predators immediately prior to the trials. Similarly important are experiments investigating how changes in the presence of noxious foods in the individual's potential diet affects that individual's level of neophobia. In related experiments, Heinrich (1988) expected to find that neophobia in ravens was associated with previous exposure to shooting, trapping, or other dangers while foraging. He found, however, that naïve and experienced ravens showed similar levels of neophobia, suggesting that the response was not facultative.

Variation in food abundance, predictability, and spatial distribution has been investigated with respect to spatial exploration (Zach and Falls, 1976) and sampling of heterogeneous resources (see Stephens and Krebs, 1986). The degree to which these factors affect the investigation of novel objects, foods, and situations would be exciting areas of future research, both within single species and across species.

3.10. Seasonal Changes in Costs and Benefits of Novelty Responses

Just as the costs and benefits of approaching novel situations vary seasonally or with life-history stage, we might also expect programmed seasonal changes in novelty responses. Mettke-Hofmann (2000b) found differences between responses of courting and breeding pairs of Red-rumped Parrots (*Psephotus haematonotus*). Breeding females in the familiar aviary investigated three novel objects more slowly, touched fewer objects, and explored for a shorter time than did pairs in courtship state, whereas exploration by males did not change from courtship to breeding. Considering the pair-unit, total duration of exploration was shorter in pairs when breeding than during courtship. Parrots in early stages of the reproductive cycle are still searching for and examining potential sites in which to nest, and their attraction to explore novel objects may well reflect this.

In the life history of many birds, migration offers a clear case of a major event that should affect the salience of novelty and have an

impact on ecological plasticity (Morse, 1980); transient birds naturally encounter more novel situations as they move between breeding and nonbreeding sites. Thus we expect that exploratory tendencies and neophobia vary along with the myriad other physiological and behavioral adjustments associated with migratory condition (Gwinner, 1996; Gwinner et al., 1985; Berthold, 1976). Surprisingly, this obvious proposition has not been studied. Similarly, changes in exploratory behavior and neophobia during the post-breeding period have not been studied in birds; this period has been hypothesized to be a critical time for exploring and selecting habitat patches for future occupation (Reed et al., 1999; Morton et al., 1991).

4. EXPLORATION IN JUVENILE BIRDS

4.1. Overview

The juvenile period provides an excellent focus for studies of exploration because at that stage such behavior is generally more frequent and conspicuous. Young birds move into an environment that is entirely novel; and, at least in altricial birds, much exploration takes place prior to attainment of self-reliance, so that classical associative learning about foods and food sources (Pellis, 1981; Duvall, 1980) is not as important as it is in adult exploration. The dramatic shift from neophilia to neophobia that attends maturation is readily explainable by simple considerations of the changes in costs and benefits of exploration. Young animals begin life with no information about their environment, so the potential benefits of exploration are great. Furthermore, parental care confers additional protection and neophobia is reduced. In contrast, in adults the benefits of exploration are greatly reduced and there is little outside protection from predation.

After rearing nearly 150 individuals of eight species of British songbirds, Barraud (1961) noted that the fear of stimuli that are "strange or of exceptional intensity" is characteristic of adult birds; but that starting at 16–18 days after hatching, passerines are highly exploratory of new objects or surroundings and adjust rapidly as compared to adults. Barraud proposed the simple hypothesis that individuals cannot differentially attend to novelty until they have familiarized themselves with the normal environment. Neophilia remains high until the overall environment becomes familiar, and a switch to neophobia occurs subsequent to the individual's becoming familiar with its natal environment. This view is substantiated in Pellis' (1981) thoroughly quantified study of
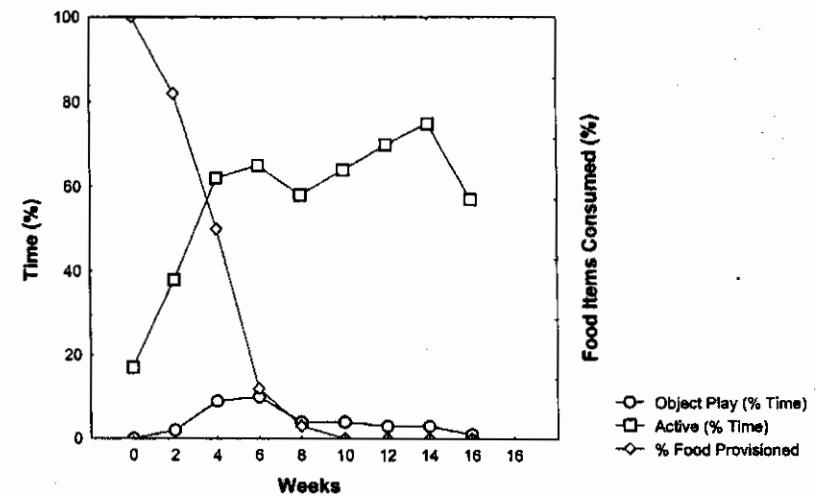

FIGURE 7. Percentege of totel observetion time spent in object exploration and other activities by Austrelian Megpies (*Gymnorhina tibicen*), plotted against number of weeks after fledging; also, percentage consumed of food items provided by parents, plotted against number of weeks after fledging (based on Pellis, 1981, with permission from Cognizant Communications Inc.).

Australian Magpies (*Gymnorhina tibicen*) (Figure 7). Pellis found that object exploration was low immediately after fledging, peaked shortly before independence, and diminished as birds entered adulthood. The timing of the magpie's peak of object exploration was consistent with what has been reported, albeit anecdotally, for other species, in which there is little exploration immediately after fledging and a high degree of exploration around the time of independence. The pattern of increasing object exploration remains, even when the amount of time spent in exploration is corrected for changes in overall activity accompanying maturation. This ontogenetic change was ascribed by Pellis to two factors: a shift in the salience of novel stimuli in changing environments and an increase in other activities, particularly foraging. The difference in exploratory behavior in altricial and precocial birds would be a fruitful area of research, since altricial birds explore their environment while still relying on adults for food.

Juvenile birds, even in precocial species, are still strongly influenced by the behavior of attending parents, which they follow and respond to. Cadieu et al. (1995) established that a short period of exposure of juvenile Canaries (*Serinus canaria*) to the consumption of a

new food by their parents was equivalent to a long period of passive familiarization in the absence of parents. Beyond this study however, the influence that parent birds have on juvenile exploration has not been systematically studied in birds; neither has the influence of parental care on the individual's responses to novelty after it has grown to adulthood, an influence that has been shown to be substantial in some primates (Clarke and Boinski, 1995).

4.2. What Do Juvenile Birds Explore?

Although intense object manipulation has been well documented in young birds, the factors that determine what they prefer to explore have received little attention. Heinrich (1995) has shown that novelty itself has a high degree of salience for young ravens. Although it has long been believed, based on anecdotal observation, that young ravens are attracted to certain kinds of objects (e.g., shiny ones), Heinrich's experiments suggest that they approach and manipulate all novel objects and that their preferences are winnowed as they mature. In an experiment on object exploration in the Chestnut-sided Warbler, Greenberg (1984c) periodically presented juvenile warblers with novel objects in addition to those regularly presented; novel objects were consistently more attractive.

Beyond a general neophilic response, few studies have examined what particular features elicit greater response in young birds and what biological significance these features might have. Smith (1973) observed that juvenile songbirds were highly attracted to novel objects, but that certain stimulus features, such as spots, tended to elicit the greatest responses. Negro et al. (1996) found that young American Kestrels (Falco sparverius) preferred to manipulate objects that resembled prey normally taken by adults (e.g., mice). Greenberg (1978b) studied the objects preferred for exploration by the highly specialized Worm-eating Warbler (Helmitheros vermivorus). On its wintering range in the Caribbean and Mesoamerica, this species consistently forages from dead leaves that hang in the forest understory. Greenberg divided juveniles into two groups, each of which was presented with nine different objects (both natural and artificial); the only objects shared between the two groups were dead leaf clusters. Individuals in each group consistently preferred to visit the dead leaves. Furthermore, different individuals, even those raised in isolation, ranked the various objects similarly in the frequency of their exploratory visits. Greenberg (1987b) hypothesized that a more specialized species might show greater stereotypic preference for objects explored than would a more generalized species.

When he compared the pattern of object exploration by the specialist wood-warbler and by a generalist, the Carolina Chickadee (Parus carolinensis), the wood-warbler indeed showed high stereotypy. The preferences of the chickadees were highly variable, particularly across rearing groups; within rearing groups, individuals converged upon similar preferences. These results suggest that the intraspecifically social chickadee is more sensitive to social facilitation in its object selection. There were no parent birds in the experiments, which leaves open the possibility that adult chickadees may have greater influence over object-exploration preferences of young than would adults of the more stereotypic wood-warbler over their young.

4.3. Object Manipulation in Young Birds: Familiarization or Practice?

The intense object exploration of juvenile birds, like that of other higher vertebrates, could have three distinct functions, each with different implications for how such exploration affects adult behavior: (1) young birds could simply be practicing adult behaviors and exercising; (2) they could be actively familiarizing themselves with their environment, a process that generates lifelong preferences that are then protected by adult neophobia; or (3) they could be exploring a wide variety of objects and potential foods and gradually winnowing their responses to only those objects of value (Chai, 1996; Heinrich, 1995). With respect to distinguishing between the first two functions, at least one study on house cats (Felis domesticus) has shown that the motor patterns exhibited when handling novel objects are distinct and identifiable from those that are used in prey-attack practice on familiar objects (West, 1977). Perhaps more detailed study of the topology of brain activity could distinguish between neophilia and object play.

Few studies have focused on long-term consequences of object exploration during the juvenile period. The experiments of Grünberger and Leisler (1993), described above, established that Coal Tits reared in a particular environment prefer to forage near, and show less neophobia toward, objects associated with that environment. Greenberg, testing Chestnut-sided Warblers (Greenberg, 1984c), Worm-eating Warblers (Greenberg, 1987b), and Melospiza sparrows (Greenberg, 1992) in their first autumn of life, investigated the preference for approaching objects that the subject individuals had investigated during juvenile exploration. The results were particularly clear for the sparrows and Chestnut-sided Warblers. After two weeks spent in the absence of previously explored objects, Chestnut-sided Warblers showed much greater la-

tency to forage at in the presence of novel objects than at objects investigated earlier in life. More important, after four months of nonexposure, Chestnut-sided Warblers in multiple-choice preference tests still preferred to feed at the once familiar objects. In experiments of this same kind, results for Song and Swamp Sparrows were similar to those for the Chestnut-sided Warbler; the behavior of Worm-eating Warblers was less conclusive.

These comprise most of the studies of the long-term effect of object exploration by juvenile birds. However, the related phenomena of diet and habitat "imprinting" have received a small amount of experimental attention. The development of adult preferences for environmental features has been thought to be analogous to the process of filial imprinting. In filial imprinting (Bateson, 1971), preferences that will be important when young birds become adults (mate choice and other associations) are developed on the basis of the following responses of juvenile birds during a brief sensitive period; the preferences are then protected by neophobia. As in other forms of novelty responses, juvenile following behavior is capable of being directed toward a wide variety of moving objects, and novelty itself has a high degree of salience. Still, not all novel objects are equal in eliciting the following response, and considerable research has been directed at determining the stimulus features that elicit the strongest response.

There have been few experimental assessments of either habitat or dietary imprinting. Although the concept of dietary imprinting was suggested by the experiments of Rabinowitch (1968, 1969) and Capretta (1969), Doherty and Cowie (1994) specifically investigated the question whether exposure of juvenile birds to a food type leads to a long-lasting preference. For eight weeks juvenile Canaries were fed either a single seed type or a mixture of four seed types. For an additional 15 weeks both treatment groups were fed only the mixture, after which they were given preference tests. Birds of the group that was reared on a single seed type showed a strong tendency to prefer that type. On the other hand, members of the group fed the mixed diet during the original eight weeks developed a consistent order of preference among the four seed types; this preference all but disappeared by the end of 23 weeks.

Glück (1984) most convincingly established the efficacy of habitat imprinting, a concept first suggested by Thorpe (1945) and subsequently investigated by Klopfer (1963). He trapped 4-week-old fledgling Linnets (*Acanthis cannabina*) and placed them in aviaries containing spruce or cherry foliage or plastic branches, then withdrew these perch types for six months. When he gave the birds the opportunity to choose to perch on any of these foliage types, he found they had a strong initial prefer-

ence for the familiar foliage. Results of further work on hand-raised nestlings were consistent with these, with the additional observation that birds responded to presentations of unfamiliar foliage with elevated heart rate. This suggests that neophobia operated to reinforce the preference for the foliage experienced early in life (Glück and Leisler, 1994).

4.4. The Effect of Diverse and Depauperate Early Environment on Adult Neophobia

It has long been suggested that, apart from the specific experience animals have with particular foods or objects, the overall stimulus richness of the early environment will have an effect on adult neophobia (Kuo, 1967; Menzel et al., 1961). This hypothesis has clear implications that neophobia is an evolved trait, because it would suggest that reduced neophobia is the result of a more diverse experience and not its cause. Still, it should be remembered a fledgling's early environment is created in part by the habitat selection of its parents and by the following and exploratory behavior of the fledgling itself. Most research in this area has been directed toward neophobia as it relates to preference for flavors among domesticated animals. The results suggest that animals reared with exposure to a greater variety of foods do show reduced neophobia of food with a novel taste (see review in Corey, 1977). In terms of mechanism, it has proved difficult to determine whether animals change their overall response to novelty as a result of early exposure to more diverse flavors or foods, or whether they simply show stimulus generalization to the greater range of flavors or foods to which they were exposed.

Raach and Leisler (1989) investigated the richness of the early environment and its importance for neophobia and exploration. They transferred hand-raised Moustached Warblers immediately after fledging into deprived holding conditions (containing only standard perches) or enriched conditions (perches plus cardboard tubes, wood-wool, ribbons, etc.) and kept them there for at least seven weeks. Subsequent experiments showed that birds raised under deprived conditions fed significantly less promptly from novel food containers than birds raised under enriched conditions. The same individuals were tested for their exploratory behavior. The investigators measured the frequency of approach to and the duration of exploration of eight novel objects containing food, and they detected no influence of earlier experience on exploration. Jones (1982) did find an influence of experience on exploration by domestic chicks raised in either bare or enriched boxes. He then placed the 7-day-old chicks individually in empty boxes and allowed a 2-minute acclimatization period before opening a hole in one wall of

the box. Birds raised in the enriched box showed shorter latencies to enter the hole than birds raised in the bare environment.

Even a short exposure to different environments can influence latency to approach a novel object. Saegert and Rajecki (1973) compared approach latencies among three groups of chicks that had been exposed briefly to situations that varied in novelty. Prior to testing, which took place at the age of 17 hours post-hatching, one group had experienced a slightly novel environment; a second group had faced a highly novel environment; and a third group had not been exposed to novelty. When tested for latency to approach a yellow card, a highly novel object, the groups differed significantly, with the shortest latencies in the group that had been exposed to the highly novel environment.

In one of the few studies of neophobia and exploration not involving food or foraging site, Schaden (1993) examined the responses of Barn Owls (*Tyto alba*) that he raised in captivity in housing environments that differed in stimulus richness. Treatment groups of adult owls were tested for their preference for nesting or roosting enclosures (housing). Owls that had been raised in one housing type, from which they were unable to see other types, avoided all but the type of housing they had been exposed to when young. Owls reared in a type that provided visual contact with another type readily explored, courted, and roosted in the housing of other types, but nevertheless nested in the type in which they had been reared.

5. COMPARATIVE STUDIES OF NEOPHOBIA AND EXPLORATION

5.1. Taxonomic Comparisons

Many of the early comparative studies of exploration were conducted across a broad taxonomic range. Wünschmann (1963) investigated object exploration in adult Jackdaws, subadult 8-month-old quail and 12-week-old domesticated hens. He presented the Jackdaws with objects having both familiar and novel patterns (stripes, stars, etc.). Similarly, he offered the hens and the quail familiar and novel patterns painted on a wall in an arena that was divided into 12 compartments. All three species investigated the novel patterns more frequently than the familiar, but each in its own way: Jackdaws manipulated the objects very intensively with bill and feet; hens pecked repeatedly and precisely at the patterns; quail investigated the stimuli only visually but visited the compartments with the novel patterns more frequently and

for a longer time. At the time of the study, great emphasis was put on phylogenetic development and the author suggested that the more recently derived taxon—in this case the corvid—was more exploratory. It is perhaps more plausible that younger individuals belonging to ecologically more generalized species were the most exploratory. Even more parsimoniously, perhaps the three species groups were equally exploratory but varied in using the mode of exploration consistent with their different foraging behaviors. This last possibility presents a problem in interpreting many studies of exploration, since the results are often based on amount of actual contact with the novel object and exclude visual inspection.

Glickman and Sroges (1966) conducted the pioneering comparative work on exploration in a number of species of reptiles and mammals, with particularly good representation from carnivores, rodents, and primates. The tests were carried out in zoological parks. Each individual was presented the same novel objects in its home cage while observers registered the number, type, and duration of object-contacts. The authors found that the environment in which each species normally foraged predicted the individual's reactivity better than did its phylogenetic relationships. Species that find food by manipulating their environment extensively reacted more to the objects than did other species. Russel and Pearce (1971), working with marsupials, and Torigoe (1985), comparing 72 species of primates, confirmed these findings.

In one of the most thorough comparative studies of birds, Mettke (1995) investigated object exploration in captive parrots of 61 species. She introduced a novel object (a wooden ring) into familiar aviaries. The latency between introduction of the object and first tactile contact by each species was correlated with 17 variables comprising a range of ecological conditions of the species in the wild. Short latencies were associated with the following species characteristics: inhabiting forest edge; feeding on nectar, fruits, or nuts; living on islands; and (nonsignificantly) sedentary status. Furthermore, duration of exploration was positively correlated with the habit of feeding on nuts.

Most of the correlations between environmental variables and exploratory behavior were robust when phylogenetic controls were applied (Mettke-Hofmann et al., in preparation). They also supported some a priori ecological predictions, e.g., that latency should be less in parrots from variable and complex environments (forest edge), where the payoff of exploration should be greater, than in stable and less complex environments. Forest edge is a very complex and variable habitat type, with diverse strata and various opportunities for hiding and locations for finding food.

This influence that the food type of a parrot species has on the latency to explore by a member of that species is in concordance with results of other investigations. Exploration can supply information about places to find cryptic food or about the size of food type that is most profitable to handle (Greig-Smith, 1987a; McNamara and Houston, 1985). For example, time required to open shells of crabs can vary depending on their size and thickness (Elner and Hughes, 1978). Parrots that eat nuts manipulate new objects longer than do parrots with other food preferences (Mettke, 1995). Nectar, fruits, and nuts vary in abundance over time and space and require more searching than do other food types. Greater exploration is characteristic of primate taxa that feed on nuts or forage for insects embedded in bark or dead leaf clusters; a good example of this is the higher degree of manipulative exploration found in Cercopithecinae as compared to Colobinae (Clarke and Linburg, 1993; Torigoe, 1985; Glickman and Sroges, 1966). Greenberg (1987b) in his study of the development of dead-leaf foraging by Worm-eating Warblers, which forage for hidden prey, noted that the highly exploratory behavior characteristic of young warblers continued into adulthood.

Finally, the hypothesis that birds that are resident for long periods are more exploratory than nomads received support from the parrot study of Mettke-Hofmann (2000a). She tested object exploration by simultaneously presenting three novel objects to individuals of six closely-related species of Loriini and four species of Platycercini; each test was performed on resident and nomadic species in their familiar aviaries. More resident individuals investigated objects and showed shorter latencies to make contact with them than did nomadic confirming the prediction that residents react more readily to environmental changes.

5.2. The Neophobia Threshold Hypothesis

The Neophobia Threshold Hypothesis (NTH, Greenberg 1990b) remains one of the few attempts at a more general explanation for ontogenetic and phylogenetic variation in novelty responses. The threshold is an ecological one. However, it fits well with current hypotheses that neophobia and other expressions of temperamental timidity are related to a lower threshold of response within neural pathways of the hypothalamic-limbic and sympathetic nervous systems (Kagan et al., 1988). The NTH was based on studies of congeneric wood-warblers (Dendroica) and sparrows (Melospiza), but is supported by comparative studies of generalist and specialist primates as well (Tardiff, 1994; Milton, 1981). The hypothesis does not address variation in the nature of early exploration; rather, it focuses on the effect of interspecific variation in the intensity of adult neophobia, and it also recognizes that early exploration conveys a familiarity that has salience into adulthood. We present the hypothesis as Greenberg (1990a) stated:

1. Birds respond differentially to novel stimuli.
2. Adult birds often respond with acute stress, which leads to avoidance and excitement.
3. The attraction of a potential food source and the fear response induced by novelty produce a tension, which is ultimately resolved either through habituation or by avoidance. The greater the intensity of the initial fear response, the less likely the individual will explore or feed at the novel stimulus.
4. The fewer novel microhabitats or food items a bird approaches, the fewer will be available for incorporation into its foraging repertoire. The result will be observed as reduced ecological plasticity.
5. Exploration is largely relegated to the juvenile period, in which fledgling birds are attracted to a wide variety of novel objects. Neophilia and exploration in juveniles establish preferences that are protected by neophobia later in life (Galef and Clark, 1971). Variation in neophobia determines how stereotyped these preferences remain. Neophilia in juvenile birds makes this period particularly important for shaping the foraging niche of their species. The more intense the neophobia of adults, the more important is the period of early exploration. (Filial imprinting is based on early neophilia, followed by extreme neophobia [Bateson, 1971].)
6. Although neophobia may be ameliorated by environmental, social, or internal-state factors, the response of individuals under similar and ordinary conditions is heritable, and differences among species tested under similar conditions are largely genetically based.

If supported, the NTH provides a relatively simple behavioral mechanism underlying ecological adaptability. Still, it is not a causal hypothesis, but one that describes and relates a species' ecological and behavioral characteristics. High neophobia could be selected for either by the benefits of specialization (higher efficiency, reduced interspecific competition, etc.) or by the costs of encountering dangerous foods or predators (Greenberg, 1983). Either way, the birds would be expected to exhibit less ecological plasticity.

Greenberg compared neophobia in the Chestnut-sided and Bay-breasted Warblers, whose winter ecology had been studied in the tropical forests of Panama (Morton, 1980; Greenberg, 1984a). When compared with the Chestnut-sided Warbler, the Bay-breasted Warbler showed greater ability in the forest locations it searched for insect prey, a greater tendency toward incorporating a variety of noninsect plant foods (mainly fruit), and a strong tendency to engage in novel or innovative (*sensu* Lefebvre *et al.*, 1997) foraging behaviors. In experiments with captives, Greenberg (1984b, 1983) found that Chestnut-sided Warblers showed much greater latency than the Bay-breasted Warblers to feed at novel objects (see Figure 8 and Figure 9a).

Emberizids of the genus *Melospiza* provide a second comparison between an ecologically plastic and a more specialized species. The
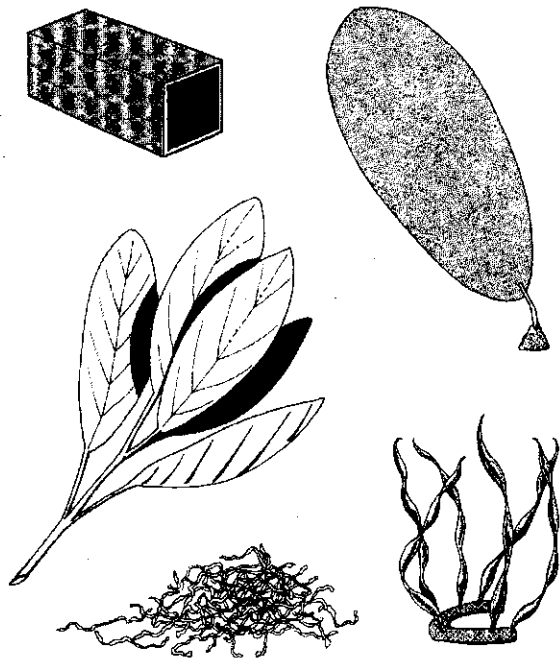

FIGURE 8. Sample of novel objects used in wood-warbler and sparrow experiments. Clockwise from upper left: black box, orange construction-paper leaf, green chenille stems, Easter grass (strips of colored plastic), vinyl leaves. These objects and others were placed next to familiar feeding locations of captive and wild birds. Object neophobia was determined by increases in latency to feed and decreases in feeding rate (Greenberg, 1990b, with permission of Academic Press).
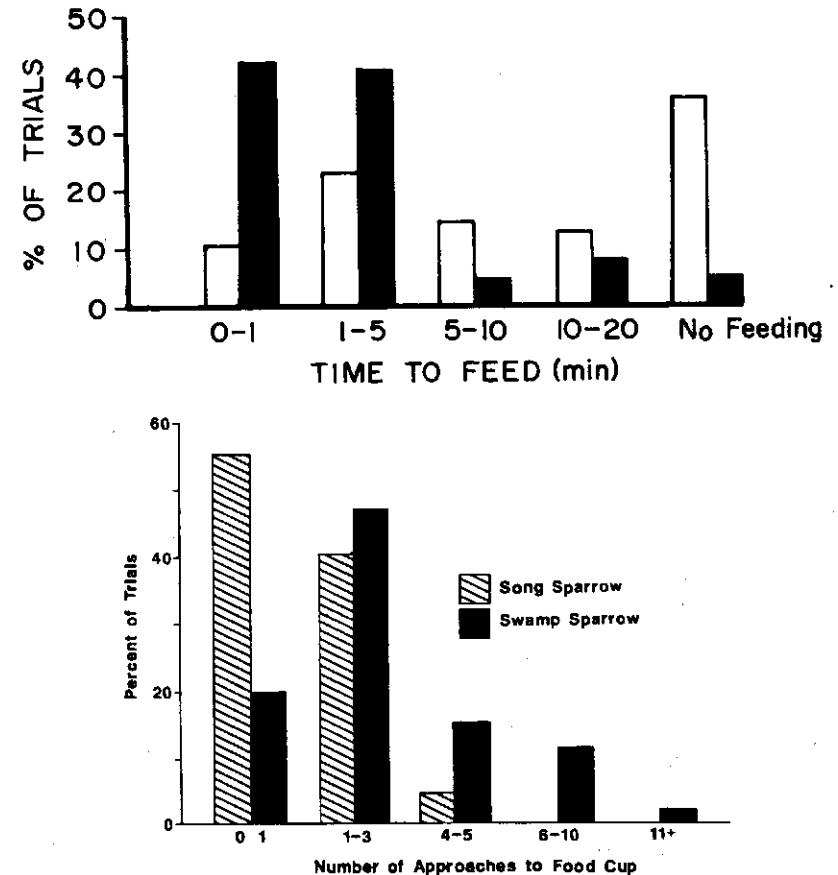
FIGURE 9. Difference in latency to feed by congeneric specialist and generalist species. Upper panel: percentages of trials falling in different latency classes for immature Bay-breasted Warbler (*Dendroica castanea*) (white bar, n = 8) and Chestnut-sided Warbler (*D. pensylvania*) (black bar, n = 7) feeding at food cups next to novel objects (n = 8) (based on Greenberg, 1984b, copyright American Psychological Association). Lower panel: distribution of number of approaches by wild-caught immature Swamp Sparrows (*Melospiza georgiana*, n = 11) and Song Sparrows (*M. melodia*, n = 10) prior to feeding at food cups next to novel objects (n = 6) (based on Greenberg, 1990a, with permission from Academic Press).

Song Sparrow is widely distributed, is often associated with anthropogenic habitats, and is a frequent colonizer of small islands, where habitat niche shifts are commonly reported (Morse, 1977; Yeaton and Cody, 1973). The Swamp Sparrow is more specialized on shrub-wetlands, showing little evidence of an ability to colonize novel habitats (Miller, 1942). Greenberg conducted experiments on neophobia of free-living birds at feeding stations and wild-caught immatures and hand-raised immatures in the laboratory. In the field experiment (Greenberg, 1989) a series of novel objects was alternately placed in and removed from feeders to which sparrows had been attracted for several weeks, and the visits of individuals of a species were recorded when each object was present or absent. The number of Song Sparrow visits was similar for the experimental (object present) and control trials, but the visitation rate of Swamp Sparrows consistently declined at each presentation of the novel object.

In the experiments on wild-caught immatures, a series of novel objects was presented next to food cups in familiar cages, and the increased latency and number of approaches before feeding were measured (Greenberg, 1990a). Both measures were greater for Swamp Sparrows (Figure 9b). In standard feeding-latency experiments with sparrows hand-raised from the nestling stage (Greenberg, 1992), two sets of test objects were presented at feeding sites, a set the sparrows had experienced during rearing and a novel set. Contrary to the predictions of the NTH, Song Sparrows showed significantly greater neophobia than Swamp Sparrows. These experiments suggest that it may be the early environment of Song Sparrows, rather than any innate difference in temperament, that causes the interspecific difference in neophobia between individuals that have been reared in the wild.

Mettke (1995), in her study of parrots, tested for neophobia in 51 of the 61 species whose exploratory behavior had also been tested. One day after a day on which subjects were presented only with food in a feeding dish, they were presented with that dish accompanied by a familiar object (a second, empty feeding dish) or a novel object (a cotton mop). Latencies to feed on the second day (after subtracting feeding latency on the first day) were again correlated with ecological variables. In the novel-object situation, latencies were short in species that occupy several habitat types or that lived on islands. Latencies were long in species living in savannas (Mettke-Hofmann, unpublished). Species inhabiting simple and constant habitats like savannas may show high neophobia because changes there are more prominent and hence more frightening than in complex and variable habitats.

Heinrich et al. (1995) reported that adult Common Ravens show greater fear at novel baits than do other, sympatric corvids, the Blue Jay and Common Crow (Corvus brachyrhynchos). The greater neophobia of ravens may be inconsistent with the NTH because in many areas ravens occupy a relatively narrow range of habitats with limited human disturbance as compared with the habitats of the other corvids mentioned. Ravens apparently behave both as carcass specialists and, at times, as omnivorous dietary generalists. What may prove interesting is the recent expansion of some California raven populations, fueled primarily by a rapid increase in use of foods generated by humans, particularly from farms and garbage dumps (Boarman and Barry, 1995). These populations are genetically distinct from other raven populations (Fleischer and Omland, pers. comm.), and in light of the work of Heinrich et al. (1995) on eastern North American ravens they might prove to be a fruitful subject for the study of neophobia.

Two other recent studies are of note. First, as part of an investigation of specialized adaptations for learning, Seferta (1998) compared object neophobia in two species of columbids, the Rock Dove (Columba livia) and Zenaida Dove. In tests of isolated captives, the Rock Dove was considerably and significantly less neophobic than the Zenaida Dove. This result can be interpreted as related to the greater ecological adaptability of the Rock Dove and to its 5,000-year history of domestication. Second, in field tests in Barbados, Webster and Lefebvre (2000) found that the dietary generalist, the Lesser Antillean Bullfinch (Loxigilla noctis), showed less aversion to feeding at novel objects than did the more specialized nectarivore, the Bananaquit (Coereba flaveola). This study focused on feeding neophobia, and it is in this context that Bananaquits can be considered more ecologically specialized than Bullfinches. However, at a different ecological scale, the Bananaquit is a habitat generalist and a successful colonizing species. Comparisons of these species would provide a good opportunity to study whether novelty responses play different roles at these two levels of ecological decision making.

The NTH focuses on differences in response to novelty, but it does not address the possible role of differences in the ability to discriminate between the novel and the familiar. Beissinger et al. (1994) examined responsiveness to novel food items as a possible proximate mechanism underlying the extreme dietary specialization of the Snail Kite. This kite forages almost exclusively on a particular species of Apple Snail (Pomacea doliodes). In field trials, 12 kites were offered an unfamiliar congeneric snail (P. urceus), which differs only slightly from P. doloides. Only seven of the kites handled the novel snails, and they consumed a total of only four snails. The kites also exhibited ambivalence behaviors

(escape, preening, etc.) described by Coppinger (1969, 1970). The most unusual aspect of this result is that it evidently was caused by a very small morphological difference between the familiar and unfamiliar species. Perhaps what distinguishes the Snail Kite as an extreme specialist is its sensitivity to small changes in stimulus.

5.3. Neophobia and Neophilia in Island Populations

Islands have often provided a natural laboratory for study of the evolution of ecological and morphological traits, and we believe they are potentially important for testing ideas about the evolution of exploration and novelty responses. Several factors should favor exploration on islands (Mettke-Hofmann, 1999): (1) reduced predation pressure on islands decreases costs of exploration (Blazquez et al., 1997); (2) less interspecific competition (e.g., Löfgren, 1995; Baker-Gabb, 1986; Mac-Arthur et al., 1972; Diamond, 1970) reduces the chance that other species are already exploiting any newly discovered resources; and (3) temporary food shortages or high levels of intraspecific competition can be survived by prompt exploration of new resources (Blondel et al., 1988; Crowell, 1983). Less work has been done on neophobia in island populations, but it has been suggested that many island species display only slight neophobia (Grant, 1998).

Haemig (1989) compared exploratory behavior of the Island Jay (*Aphelocoma insularis*), which inhabit the Channel Islands of California, and the mainland California Jay (*A. californica*). The island population occupies a broader range of habitats than the mainland population (Atwood, 1980). Haemig attracted both jays by a noise, and the Island Jays approached more closely than their mainland relatives and remained for a longer time at the source of noise. In her general survey of 61 parrot species, Mettke (1995) found that island species were significantly more exploratory then mainland species. In a more focused comparison within the genus *Chalcopsitta*, she found that the more exploratory island species (*C. cardinalis*) has a broader food niche than the less exploratory, closely-related mainland species (Mettke-Hofmann, 1999).

Differences in neophobia and neophilia between island and mainland forms could be associated with adaptive behavioral changes in colonizing populations (Mettke-Hofmann, 1999). It is also possible that island species, whose populations may have arisen from individuals with greater exploratory tendencies and reduced neophobia, are more successful in surviving as colonists than related species without these attributes. Morse (1971, 1977) found an interesting correlation in parulid

wood-warblers: The most successful island colonizers are species from edge habitats. Similarly, parrot species inhabiting the forest edge are more exploratory than species living in other habitats (Mettke, 1995). It would be worthwhile to investigate whether the colonizing parulids from edge habitats are also more exploratory.

Because this discussion is an initial approach to the relationship between exploratory behavior and island colonization, it has been simplistic. In fact, many island species show no indication of responding, in ways relevant to this chapter, to the insular change in resources, competition, and predation. In general, species in this group have relictual distributions on land-bridge islands (Greenberg, 1990b); but even in species that have colonized oceanic islands, changes in plasticity and hence exploratory behavior may vary with the time a taxon has been on an island. Further, it has been shown in at least one case that what appears to be a generalist island species is actually composed of specialists with different specializations (Werner and Sherry, 1987). Despite these complexities, we believe that comparisons of mainland and island congeners can help test whether environments affect novelty responses in ways that are consistent with theory. We note, however, that because food distribution, competitive environment, and predation often covary on islands, environmental causation of differences in neophilia and neophobia will be difficult to establish. Practicing ecologists will be familiar with this problem.

6. CONCLUSIONS AND FUTURE DIRECTIONS

Birds react to novel objects, foods, or situations with a combination of curiosity, aversion, and indifference; these responses could have major implications for how an animal deals with a variable and changing world. The behavioral data suggest that attraction to explore novelty and aversion to avoid it are two distinct responses that interact, often resulting in responses striking in their ambivalence. Neophilia is strongly related to age, with juvenile birds showing the greatest attraction to manipulate and otherwise interact with novel objects. Strong neophilia is rarely observed in adults, with the exception of species that forage in complex environments or seek hidden prey. Nonetheless, a measure of neophilia is part of the normal repertoire of most adult birds. Neophobia is characteristic of adults and appears to be related to the degree of ecological specialization of the species and the level of danger from predation and poisonous prey. Intraspecific variation also occurs;

it may be an intrinsic trait of the individual, or it may be facultatively related to dominance status, condition, food distribution, and predator abundance.

The NTH provides a general framework for looking at intrinsic interspecific differences in novelty responses. Under this hypothesis, juvenile neophilia is followed in adults by a variable degree of neophobia. Ecological specialization is largely the result of, and increases with, the intensity of the adult neophobia response. In its present form, the NTH does not suggest what factors might be most important in selecting for differences in neophobia. Also, the hypothesis needs modification to reflect the fact that potentially conflicting selection pressures might independently shape the exploratory drive and neophobia. Finally, the hypothesis is inherently a comparative one, and testing it will require much more rigorously gathered comparative data with better phylogenetic controls.

The scarcity of comparative studies of novelty responses, particularly of wild birds, is surprising, considering that in the past two decades researchers have called for a more ecological approach to the investigation of animal learning mechanisms; an ecological approach should involve just such comparative studies (e.g., Kamil and Yoerg, 1982; Johnston, 1981). Furthermore, the natural world is full of examples of closely related species that differ in ecological plasticity, and each ecological comparison is a potential goldmine for exploring the hypotheses presented here, as well as for formulating hypotheses not yet developed. Among closely related species, do those displaying greater foraging or habitat specialization tend to show greater neophobia than their generalist relatives? Are interspecific differences in exploration and neophobia genetically based? Do species that have been shown in the field to incorporate new and unusual foraging patterns differ in their intrinsic neophobia and neophilia from related species for which such new behaviors have not been documented?

There are also opportunities to understand the adaptive significance of novelty responses by examining intraspecific geographic variation in individuals. In particular, island–mainland comparisons seem promising. Will future studies confirm the idea that occupation of islands reduces neophobia and enhances neophilia? Or will we find that species whose neophilia is high and neophobia low are predisposed to success when they colonize islands?

Increasing attention is being paid to the evolutionary significance of temperament differences in animals, particularly as such differences relate to social behavior. This opens up exciting research questions, including the following: Is intraspecific variation in exploration and neophobia related to other behavioral attributes of individuals, such as dominance or wariness in the presence of predators? Is variation in neophobia and exploratory tendencies greater in social than in asocial species? If such variation is substantial, is it facultative or does it have an intrinsic basis?

What seems to be consistent interindividual variation may actually be related to ontogenetic or seasonal changes, which raises such questions as these: Does familiarization as a result of juvenile exploration have a long-term influence on plasticity of diet, foraging microhabitat, and habitat selection? How much does the stimulus diversity of the natal environment influence exploration and neophobia later in life? What determines what young birds choose to explore and how do these preferences relate to the ecological problems confronted by adults? Do migratory species show alternating changes in exploratory tendencies and neophobia between periods of migration and residency?

Finally, as we move toward developing more evolutionary models for characteristics of temperament, such as curiosity and neophobia, we need a greater understanding of the physiological mechanisms underlying these characteristics. For example, what role do brain structures and neural pathways have in shaping novelty responses? Answers to such questions will bring us closer to understanding how selection has shaped these traits, which have such clear implications for the behavioral ecology of avian species.

REFERENCES

Allen, J. A., 1988. Frequency-dependent selection by predators, *Phil. Trans. Roy. Soc. Lond. Ser. B.* **319**:485–503.

Andrew, R. J., 1972, Changes in search behaviour in male and female chicks following different doses of testosterone, *Anim. Behav.* **20**:741–750.

Andrew, R. J., and Rogers, L. J., 1972, Testosterone, search behaviour and persistence, *Nature* 237:343–346.

Atwood, J. L., 1980, Social interactions in the Santa Cruz Island Scrub Jay, *Condor* 82:440–448.

Baker-Gabb, D. J., 1986, Ecological release and behavioural and ecological flexibility in Marsh Harriers on islands, *Emu* 86:71–81.

Barraud, E. M., 1961, The development of behaviour in some young passerines, *Bird Study* 8:111–118.

Barrows, E. M., 1995, *Animal Behaviour Desk Reference*, CRC Press, Boca Raton, FL.

Barrows, E. M., Acquavella, A. P., Weinstein, P. J. S., and Nosal, R. E., 1980, Response to novel food in captive, juvenile Mockingbirds, *Wilson Bull.* 92:399–402.

Bateson, P. G., 1971, Imprinting, in: *Ontogeny of Vertebrate Behavior*, (H. Moltz, ed.), Academic Press, New York, pp. 369–387.

Beesher, J., Jensen, H. C., and Bevins, R. A., 1999, Dopamine antagonism in a novel-object preference and a novel-object place conditioning preparation with rats, *Behav. Brain Res.* 103:35–44.

Beissinger, S. R., Donnay, T. J., and Walton, R., 1994, Experimental analysis of diet specialization in the Snail Kite: The role of behavioral conservatism, *Oecologia* 100:54–65.

Benjamin, J. L., Li, C., Patterson, B. D., Greenberg, D. L., Murphy, D., and Hammer, H., 1996, Population and familial association between the D4 dopamine receptor gene and measures of novelty seeking, *Nature Genet.* 12:81–84.

Berlyne, D. E., 1950, Novelty and curiosity as determinants of wild and laboratory rats, *Br. J. Psych.* 41:68–80.

Berthold, P., 1976, Animalische und vegetabilische Ernährung omnivorer Singvogelarten: Nahrungsbevorzugung, Jahresperiodik der Nahrungswahl, physiologische und ökologische Bedeutung, *J. Ornith.* 117:145–209.

Bevins, R. A., and Bardo, M. T., 1999, Conditioned increase in place preference by access to novel objects: Antagonism by MK-801, *Behav. Brain Res.* 99:53–60.

Birke, L. I. A., and Archer, J., 1983, Some issues and problems in the study of animal exploration, in: *Exploration in Animals and Humans* (J. Archer and L. Birke, eds.), Workingham Press, Berkshire, England, pp. 1–21.

Blazquez, M. C., Rodriguez-Estrella, R., and Delibes, M., 1997, Escape behaviour and predation risk of mainland and island Spiny-tailed Iguanas (*Ctenosaura hemilopha*), *Ethology* 103:990–998.

Blondel, J., Chessel, D., and Frochot, B., 1988, Bird species impoverishment, niche expansion, and density inflation in Mediterranean island habitats, *Ecology* 69:1899–1917.

Boarman, W. I., and Barry, K., 1995, Common Ravens in the southwestern United States, 1968–92, in: *Our Living Resources* (E. T. LaRoe, ed.), National Biological Service. Washington, D.C., pp. 73–75.

Boisy, A., 1995, Fear and fearfulness in animals, *Quart. Rev. Biol.* 70:165–191.

Budaev, S. V., 1997, Personality in the Guppy (*Poecilia reticulata*): A correlational study of exploratory behavior and social tendency, *J. Comp. Psych.* 111:399–411.

Cadieu, J. C., Cadieu, N., and Medioni, J., 1995, Parental influence on food familiarisation in the fledgling Canary (*Serinus canarius*) and its long-term effect, *Ethol. Ecol. Evol.* 7:265–270.

Caldwell, G. S., and Rubinoff, R., 1983, Avoidance of venomous sea snakes by naïve herons and egrets *Auk* 100:195–198.

Capretta, P. J., 1969, The establishment of food preferences in chicks, *Gallus gallus*, *Anim. Behav.* 17:229–231.

Chai, P., 1996, Butterfly visual characteristics and ontogeny of responses to butterflies by a specialized tropical bird, *Biol. J. Linn. Soc.* 59:37–67.

Chamove, A. S., 1983, Role of dominance on macaque response to novel objects, *Motivation and Emotion* 7:213–228.

Chance, M. R. A., and Meade, A. P., 1955, Competition between feeding and exploration in the rat, *Behaviour* 8:174–182.

Clarke, A. S., and Boinski, S., 1995, Temperament in nonhuman primates, *Am. J. Primat.* 37:103–125.

Clarke, A. S., and Linburg, D. G., 1993, Behavioral contrasts between male cynomlgus and Lion-tailed Macaques, *Am. J. Primat.* 29:49–59.

Clarke, A. S., Mason, W. A., and Moberg, G. P., 1988, Differential behavioral and adrenocortical responses to stress among three macaque species, *Am. J. Primat.* 14:37–52.

Coleman, K., and Wilson, D. S., 1998, Shyness and boldness in Pumpkinseed Sunfish: Individual differences are context-specific, *Anim. Behav.* 58:927–936.

Coleman, S. L., and Mellgren, R. L., 1994, Neophobia when feeding alone and in flocks in Zebra Finches *Toeniopygia guttata*, *Anim. Behav.* 48:903–907.

Coppinger, R. P., 1969, The effect of experience and novelty on avian feeding behaviour with reference to the evolution of warning colouration in butterflies. Part I. Reactions of wild caught Blue Jays to novel insects. *Behaviour* 35:45–60.

Coppinger, R. P., 1970, The effect of experience and novelty on avian feeding with reference to the warning coloration of butterflies. II. Reactions of naïve birds to novel insects, *Am. Nat.* 194:323–337.

Corey, D. T., 1977, The determinants of exploration and neophobia, *Neurosci. Biobehav. Rev.* 2:235–253.

Cowan, P. E., 1976, New object reaction of *Rattus rattus*: the relative importance of different cues, *Behav. Biol.* 16:31–44.

Cowan, P. E., and Barnett, S. A., 1975, The new object and new place reactions of *Rattus rattus* (L.), *Zool. J. Linn. Soc.* 56:219–234.

Crowell, K. L., 1983, Islands—insight or artifact?: Population dynamics and habitat utilization in insular rodents, *Oikos* 41:442–454.

Daugherty, C. H., Gibbs, G. W., and Hitchmough, R. A., 1993, Mega-island or microcontinent? New Zealand and its fauna, *Trends Ecol. Evol.* 8:437–442.

Deckert, G., and Deckert, K., 1982, Spielverhalten und Komfortbewegungen beim Grünflügelara, *Ara chloroptera*, *Bonn. Zool. Beitr.* 33:269–281.

DesForges, M. F., and Wood-Gush, D. G. M., 1975, A behavioural comparison of domestic and Mallard ducks, *Anim. Behav.* 23: 692–697.

Diamond, J. M., 1970, Ecological consequences of island colonization by southwest pacific birds, I. Types of niche shifts, *Proc. Nat. Acad. Sci.* 87:529–536.

Doherty, S., and Cowie, R. J., 1994, The effects of early feeding experience on long-term seed choice by Canaries (*Serinus canaria*), *Ethology* 97:177–189.

Drent, P. J., 1997, Realised heritability of a behavioural syndrome in the Great Tit, *Progress Report of the Netherlands Institute of Ecology* 44–47.

Drent, P. J., and Marchetti, C., 1999, Individuality, exploration and foraging in hand raised juvenile Great tits. *Proc. 22nd Intern. Ornith. Congr.*, (N. Adams, and R. Slowtow, eds.), University Natal, Durban, pp. 896–914.

Duvall II, F., 1980, Social and object interactions of juvenile Rooks (*Corvus frugilegus*) and Hooded Crows (*C. corone cornix*), *Verh. Dtsch. Zool. Ges.* 332.

Ebstein, R. P., Novick, O., Umansky, R., Priel, B., Osher, Y., Blaine, D., Bennett, E. R., Nemanov, L., Katz, M., and Belmaker, R. H., 1996, Dopamine receptor (D4DR) exon III polymorphism associated with the human personality trait of novelty seeking, *Nature Genet.* 12:78–80.

Elner, R. W., and Hughes, R. N., 1978, Energy maximisation in the diet of the Shore Crab, *Carcinus maenas*, *J. Anim. Ecol.* 47:103–116.

Franchina, J. J., Johnson, L. J., and Leynes, P. A., 1994, Roles of visual and taste cues in ingestional neophobia: Response latency effects in chicks (*Gallus domesticus*), *Anim. Learn. Behav.* **22**:341–350.

Galef, Jr., B. J., 1993, Functions of social learning about food: a causal analysis of effects of diet novelty on preference transmission, *Anim. Behav.* **46**:257–265.

Galef, Jr., B. J., and Clark, M. M., 1971, Social factors in the poison avoidance and feeding behavior of wild and domesticated rat pups, *J. Comp. Phys. Psych.* **75**:341–357.

Glickman, S. E., and Sroges, R. W., 1966, Curiosity in zoo animals, *Behaviour* **24**:151–188.

Glück, E., 1984, Habitat selection and the role of early experience, *Z. Tierpsychol.* **68**:45–54.

Glück, E., and Leisler, B., 1994, Ontogenetic aspects of habitat selection, *J. Ornith.* **135**:480.

Götmark, F., 1994, Does a novel bright color patch increase or decrease predation: red wings reduce predation risk in European Blackbirds, *Nature* **256**:83–87.

Gould, J. P., 1974, Risk, stochastic preferences, and the value of information, *J. Econ. Theory* **8**:64–84.

Grant, P. R., 1998, Patterns on islands and microevolution, in: *Evolution on Islands* (P. R. Grant, ed.), Oxford University Press, Oxford, pp. 1–17.

Greenberg, R., 1979, Body size, breeding habitat, and winter exploitation systems in *Dendroica, Auk* **98**:756–768.

Greenberg, R., 1983, The role of neophobia in foraging specialization of some migrant warblers, *Am. Natur.* **123**:444–453.

Greenberg, R., 1984a, The winter exploitation systems of Bay-breasted and Chestnut-sided Warblers in Panama, *Univ. Calif. Publ. Zool.* **117**:1–124.

Greenberg, R., 1984b, Differences in feeding neophobia between two species of tropical-migrant warblers (*Dendroica castanea* and *D. pensylvonica*), *J. Comp. Psych.* **98**:131–136.

Greenberg, R., 1984c, Neophobia in the foraging site selection of a neotropical migrant bird: an experimental study. *Proc. Nat. Acad. Sci.* **81**:3778–3780.

Greenberg, R., 1987a, Social facilitation does not reduce neophobia in Chestnut-sided Warblers (Parulinae: *Dendroica*), *J. Ethol.* **5**:7–11.

Greenberg, R., 1987b, The development of dead leaf foraging in a Neotropical migrant warbler, *Ecology* **88**:130–141.

Greenberg, R., 1989, Neophobia, aversion to open space, and ecological plasticity in Song and Swamp Sparrows, *Can. J. Zool.* **67**:1194–1199.

Greenberg, R., 1990a, Feeding neophobia and ecological plasticity: a test of the hypothesis with captive sparrows, *Anim. Behav.* **39**:375–379.

Greenberg, R., 1990b, Ecological plasticity, neophobia, and resource use in birds, *Stud. Avian Biol.* **13**:431–437.

Greenberg, R., 1992, Differences in neophobia between naïve Song and Swamp Sparrows, *Ethology* **91**:17–24.

Greenberg, R., 1995, Novelty responses: the bridge between psychology, behavioral ecology, and community ecology, *Trends Ecol. Evol.* **10**:165–166.

Greenberg, R., and Droege, S., 1999, On the decline of the Rusty Blackbird and the use of ornithological literature to document long-term population trends, *Conserv. Biol.* **13**:553–559.

Greig-Smith, P. W., 1987a, Persistence in foraging: when do Bullfinches abandon unprofitable seeds? *Behaviour* **103**:203–216.

Greig-Smith, P. W., 1987b, Aversion of starlings and sparrows to unfamiliar, unexpected or unusual flavours and colours in food, *Ethology* **4**:155–163.

Grünberger, S., and Leisler, B., 1990, Angeborene und erfahrungsbedingte Komponenten der Habitatwahl der Tannenmeise (*Porus ater*), *J. Ornith.* **131**:460–464.

Grünberger, S., and Leisler, B., 1993, Auswirkung der Umwelterfahrung auf die Neophobie der Tannenmeise (*Parus oter*). *J. Ornith.* **134**:352–355.

Gwinner, E., 1996, Circannual clocks in avian reproduction and migration, *Ibis* **138**:47–63.

Gwinner, E., Biebach, H., and Kries, I. V., 1985, Food availability affects migratory restlessness in caged Garden Warbler (*Sylvia borin*), *Naturwissenschaften* **72**:51–52.

Haemig, P. D., 1989, A comparative experimental study of exploratory behavior in Santa Cruz Island and mainland Scrub Jays *Aphelocoma coerulescens*, *Bird Behav.* **8**:38–42.

Hegner, R. E., 1985, Dominance and anti-predator behaviour in Blue Tits (*Parus caeruleus*), *Anim. Behav.* **33**:762–768.

Heinrich, B., 1988, Why do ravens fear their food? *Condor* **90**:950–952.

Heinrich, B., 1995, Neophilia and exploration in juvenile Common Ravens *Corvus corox*, *Anim. Behav.* **50**:675–704.

Heinrich, B., Marzluff, J. M., and Adams, W., 1995, Fear and food recognition in naïve Common Ravens, *Auk* **112**:499–503.

Hogan, J. A., 1965, An experimental study of conflict and fear: An analysis of behavior of young chicks towards a mealworm. I. The behavior of chicks which do not eat the worm, *Behaviour* **25**:45–97.

Hughes, R. N., 1997, Intrinsic exploration in animals: motives and measurement, *Behav. Proc.* **41**:213–226.

Immelmann, K., and Beer, C., 1989, *A Dictionary of Ethology*, Harvard University Press, Cambridge, MA.

Inglis, I. R., and Shepherd, D. S., 1994, Rats work for food they then reject: support for the information-primacy approach to learned industriousness, *Ethology* **98**:154–164.

Jämmrich, S., 1989, Quantitative Analyse des Verhaltens gegenüber unbekannten Objekten. Untersuchungen an Insectivore, Rodentia und Primates, *Zool. Beitr. N.F.* **32**:195–215.

Johnston, T. D., 1981, Contrasting approaches to a theory of learning, *Brain Behav. Sci.* **4**:125–173.

Jones, R. B., 1982, Effects of early environmental enrichment upon open-field behaviour and timidity in the domestic chick, *Devel. Psychobiol.* **15**:105–111.

Jones, R. B., 1986, Responses of domestic chicks to novel food as a function of sex, strain and previous experience, *Behav. Proc.* **12**:261–271.

Jones, R. B., and Andrew, R. J., 1992, Responses of adult domestic cocks and capons to novel and alarming stimuli, *Behov. Proc.* **26**:189–200.

Jones, R. B., Larkins, C., and Hughes, B. O., 1996, Approach/avoidance responses of domestic chicks to familiar and unfamiliar video images of biologically neutral stimuli, *Appl. Anim. Behav. Sci.* **48**:81–98.

Kagan, J., Reznick, J. S., and Snidman, N., 1988, Biological basis of childhood shyness, *Science* **240**:167–171.

Kegan, J., Snidman, N., and Arcus, B., 1998, Childhood derivatives of low levels of reactivity in infancy, *Child Development* **89**:1483–1493.

Kamil, A. C., and Yoerg, S., 1982, Learning and foraging behavior, in: *Perspectives in Ethology, Volume 5* (P. Bateson and P. Klopfer, eds.), Plenum Press, New York, pp. 325–362.

Katzir, G., 1982, The relationship between social structure and the response to novel space, *Behaviour* **81**:231–263.

Ketzir, G., 1983, Relationship between social structure and response to novelty, *Behaviour* **87**:183–208.

Kilhem, L., 1974, Play in Hairy, Downy, and other woodpeckers, *Wilson Bull.* **86**:35–42.

Klopfer, P. H., 1963, Behavioral aspects of habitat selection: the role of early experience, *Wilson Bull.* **75**:15–22.

Klopfer, P. H., 1967, Behavioral stereotypy in birds, *Wilson Bull.* **79**:290–300.

Kothbauer-Hellmann, R., and Winkler, H., 1991, Aufenthaltsdauern explorierender Meisen: Habitat-und Artspezifität. *J. Ornith.* **132**:329–331.

Kubat, S., 1992, Die Rolle von Neuigkeit, Andersartigkeit und sozialer Struktur für die Exploration von Objekten beim Kea (*Nestor notabilis*), Ph.D. dissertation, Universität Wien, Vienna, Austria.

Kuo, Z., 1967, *The Dynamics of Behaviour Development: An Epigenetic View*, Random House, New York.

Lahti, K., Koivula, K., and Orell, M., 1997, Dominance, daily activity, and winter survival in Willow Tits: Detrimental cost of long working hours? *Behaviour* **134**:921–939.

Lefebvre, L., Whittle, P., Lascaris, E., and Finkelstein, A., 1997, Feeding innovations and forebrain in birds, *Anim. Behav.* **53**:549–560.

Levins, R., and Lewontin, R., 1985, *The Dialectical Biologist*, Harvard University Press, Cambridge, MA.

Lima, S. L., and Dill, L. M., 1990, Behavioural decisions made under the risk of predation: a review and prospectus, *Can. J. Zool.* **68**:619–640.

Löfgren, O., 1995, Niche expansion and increased maturation rate of *Clethrionomys glareolus* in the absence of competitors, *J. Mamm.* **76**:1100–1112.

Lorenz, K., 1956, Plays and vacuum activities, in: *L'Instinct dans le comportement de animaux et de l'homme*, Fondation Singer Polignac, Masson et Cie Editerus, Paris, pp. 633–638.

Lowndes, M., and Davies, M. C., 1995, The effect of archistrial lesions on open field and fear avoidance behavior in the domestic chick, *Behav. Brain Res.* **72**:25–32.

Lowndes, M., Davies, M. C., and Johnson, M. H., 1997, Archistrial lesions impair the acquisition of filial preferences, *Eur. J. Neurosci.* **8**:1143–1148.

MacArthur, R. H., Diamond, J. M., and Karr, J. R., 1972, Density compensation in island faunas, *Ecology* **53**:330–342.

Mappes, J., and Alatalo, R. V., 1997, Effects of novelty and gregariousness in survival of aposematic prey, *Behav. Ecol.* **8**:174–177.

Marchetti, K., and Price, T., 1989, Differences in the foraging of juvenile and adult birds: the importance of developmental constraints, *Biol. Rev. Camb. Phil. Soc.* **64**:51–70.

Marler, P., 1956, Behaviar of the Chaffinch, *Behaviour* (suppl.) **5**:1–184.

Marples, N. M., and Brakefield, P. M., 1995, Genetic variation for the rate of recruitment of novel insect prey into the diet of a bird, *Biol. J. Linn. Soc.* **55**:17–27.

Marples, N. M., Roper, T., and Harper, D., 1998, Responses of wild birds to novel prey: evidence for dietary conservatism, *Oikos* **83**:161–165.

Marzluff, J. M., and Heinrich, B., 1991, Foraging by Common Ravens in the presence and absence of territory holders: an experimental analysis of social foraging, *Anim. Behav.* **42**:755–770.

Mastota, F. N., and Mench, J. A., 1994, Avoidance of dyed foods by Northern Bobwhite, *Appl. Anim. Behav. Sci.* **12**:109–119.

Mayeaux, D. J., and Mason, W. A., 1998, Development of responsiveness to novel objects in the Titi Monkey, *Callicebus moloch*, *Primates* **39**:419–431.

McLaughlin, J. F., and Roughgarden, J., 1989, Avian predatian on *Anolis* lizards in the northeastern Caribbean: An inter-island contrast, *Ecology* **70**:617–628.

McNamara, J., and Houston, A., 1985, A simple model of information use in the exploitation of patchily distributed food, *Anim. Behav.* **33**:553–560.

Menzel, E. W., Davenport Jr., R. K., and Rogers, C. M., 1961, Some aspects of behavior toward novelty in young chimpanzees, *J. Comp. Physiol. Psych.* **54**:16–19.

Mettke, C., 1993, Auftreten und Ausprägung von Explorationsverhalten bei Papageien im Ökologischen Kontext, Ph.D. dissertation, Freie Universität, Berlin.

Mettke, C., 1995, Explorationsverhalten von Papageien—Adaptation an die Umwelt? *J. Ornith.* **138**:468–471.

Mettke-Hofmann, C., 1999, Niche expansion and exploratory behavior on islands: are they linked? *Proc. 22nd Intern. Ornith. Congr.*, (N. Adams, and R. Slowtow, eds.), University Natal, Durban.

Mettke-Hofmann, C., 2000a, Reactions of nomadic and resident parrot species *Psittacidae* to environmental enrichment at the Max Planck Institut, *Int. Zoo Yearbook* **37**: 244–256.

Mettke-Hofmann, C., 2000b, Changes in exploration from courtship to the breeding state in Red-rumped Parrots (*Psephotus haematonotus*), *Behav. Proc.* **49**:139–148.

Miller, A. H., 1942, Habitat selection among higher vertebrates and its relation to intraspecific variation, *Am. Natur.* **76**:25–35.

Milton, K., 1981, Distribution pattern of tropical plant foods as an evolutionary stimulus to mental development, *American Anthropologist* **83**:534–548.

Mitchell, D., 1976, Experiments on neophobia in wild and laboratory rats: a reevaluation, *J. Comp. Phys. Psych.* **90**:190–197.

Montgomery, K. C., 1955, The relation between fear induced by novel stimulation and exploratory behavior, *Comp. Phys. Psych.* **48**:254–260.

Morse, D. H., 1971, The foraging of warblers isolated on small islands, *Ecology* **52**:216–228.

Morse, D. H., 1977, The occupation of small islands by passerine birds, *Condor* **79**: 399–412.

Morse, D. H., 1980, *Behavioral Mechanisms in Ecology*, Harvard University Press, Cambridge, MA.

Morton, E. S., 1980, Adaptations to seasonal changes by migrant land birds in the Panama Canal Zone, in: *Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation* (A. Keast and E. S. Morton, eds.), Smithsonian Institution Press, Washington, D.C., pp. 437–453.

Morton, E. S., 1998, Pairing in Mallards and American Black Ducks: a new view on population decline in American Black Ducks, *Anim. Cons.* **1**:239–244.

Morton, M. L., Wakamati, M. L., Pereya, M. E., and Morton, G. A., 1991, Post-fledging dispersal, habitat imprinting, and philopatry in a migratory sparrow, *Ornis Scand.* **22**:98–106.

Murphy, L. B., 1977, Responses of domestic fowl to novel food and objects, *Appl. Anim. Ethol.* **3**:335–349.

Negro, J. J., Bustamante, J., Milward, J., and Bird, D. M., 1996, Captive fledgling American Kestrels prefer to play with objects resembling natural prey, *Anim. Behav.* **52**: 707–714.

Nietsch, A., and Todt, D., 1985, Monopolisierung tragbarer Objekte durch juvenile Individuen bei halbfrei lebenden Berberaffen (*Macaca sylvanus*), *Verh. Dtsch. Zool. Ges.* **78**:213.

Ortega, J. C., and Bekoff, M., 1987, Avian play: evolutionary and developmental trends, *Auk* **104**:338–341.

Pellis, S. M., 1981, Exploration and play in the behavioural development of the Australian Magpie *Gymnorhina tibicen*, *Bird Behav.* **3**:37–49.

Phillips, R. E., and Youngren, O. M., 1986, Unilateral kainic acid lesions reveal dominance of right archistriatum in avian fear behavior, *Brain Res.* **377**:216–220.

Poucet, B., Durup, M., and Thinus-Blanc, C., 1988, Short-term and long-term habituation of exploration in rats, hamsters, and gerbils, *Behav. Proc.* **16**:203–211.

Raach, A., and Leisler, B., 1989, Auswirkung der Jugenderfahrung auf die Wahl von Habitatstrukturen und auf das Erkundungsverhalten des Mariskensängers (*Acrocephalus melanopogon*), *J. Ornith.* **130**:256–259.

Rabinowitch, V., 1968, The role of experience in the development of food preferences in gull Chicks, *Anim. Behav.* 16:425–428.

Rabinowitch, V., 1969, The role of experience in the development and retention of seed preferences in Zebra Finches, *Behaviour* 33:222–235.

Rana, B. D., 1989, Some observations on neophobic behaviour among House Sparrows, *Passer domesticus, Pavo* 27:35–38.

Rasmussen, D. R., and Rasmussen, K. L., 1979, Social ecology of adult males in a confined troop of Japanese Macaques (*Macaca fuscata*), *Anim. Behav.* 27:434–445.

Raudensush, B., and Frank, R. A., 1999, Assessing food neophobia: The role of stimulus familiarity, *Appetite* 32:261–271.

Reed, J. M., Boulinier, T., Danchin, E., and Oring, L. W., 1999, Informed dispersal: prospecting by birds for breeding sites, in: *Current Ornithology*, vol. 15 (V. Nolan Jr., E. D.Ketterson, and C. F. Thompson, eds.), Kluwer Academic/Plenum, New York, pp. 189–259.

Renner, M. J., 1987, Experience-dependent changes in exploratory behaviour in the adult rat (*Rattus norvegicus*): overall activity level and interactions with objects, *J. Comp. Psychol.* 101:94–100.

Renner, M. J., 1988, Learning during exploration: The role of behavioural topography during exploration in determining subsequent adaptive behaviour, *Int. J. Comp. Psych.* 2:43–56.

Renner, M. J., and Seltzer, C. P., 1991, Molar characteristics of exploratory and investigatory behaviour in the rat (*Rattus norvegicus*), *J. Comp. Psychol.* 105:326–339.

Roper, T. J., 1990, Responses of domestic chicks to artificially coloured insect prey: effects of previous experience and background color, *Anim. Behav.* 39:466–473.

Rosenzweig, M. L., 1985, Some theoretical aspects of habitat selection, in: *Habitat Selection in Birds* (M. L. Cody, ed.), Academic Press, New York, pp. 517–540.

Russel, E. M., and Pearce, G. A., 1971, Exploration of novel objects by marsupials, *Behaviour* 40:312–322.

Russell, P. A., 1973, Relationship between exploratory behaviour and fear: a review, *Br. J. Psychology* 64:417–433.

Saegert, S., and Rajecki, D. W., 1973, Effects of prior exposure to animate object on approach tendency in chicks, *Behov. Biol.* 8:749–754.

Schaden, G., 1993, Exploration and neophobia in captive Barn Owls (*Tyto alba guttata*), *Egretto* 36:67–77.

Schleidt, W. M., 1961, Reaktionen von Truthühnern auf fliegende Raubvögel und Versuche zur Analyse ihrer AAM's, *Z. Tierpsychol.* 18:534–560.

Schuler, W., 1982, Zur Funktion von Warnfarben: Die Reaktion junger Stare auf wespenähnlich schwarz-gelbe *Attrappe, Z. Tierpsychol.* 58:66–78.

Schuler, W., and Hesse, E., 1985, On the function of warning coloration: A black and yellow pattern inhibits prey-attack by naive domestic chicks, *Behav. Ecol. Sociobiol.* 16:249–255.

Schuler, C., and Roper, T. J., 1992, Responses to warning coloration in avian predators, *Advances in the Study of Behaviour* 21:111–148.

Seferta, A., 1998, *The Role of Intervening Variables in Learning Differences between Group-foraging and Territorial Columbids*, MS thesis, McGill University, Montreal.

Shettleworth, S. J., 1972, The role of novelty in learned avoidance of unpalatable "prey" by domestic chicks, *Anim. Behav.* 20:29–35.

Shettleworth, S. J., 1993, Where is the comparison in comparative cognition? Alternative research programs, *Psych. Sci.* 4:179–184.

Smith, S., 1973, Factors directing prey-attack behavior by the young of three passerine species, *Living Bird* 12:57–67.

Smith, S., 1975, Innate recognition of coral snake pattern by a possible avian predator, *Science* 187:759–760.

Stamps, J. A., 1987, The effect of familiarity with a neighborhood on territory acquisition, *Behav. Ecol. Sociobiol.* 21:273–277.

Stephens, D. W., and Krebs, J. R., 1986, *Foraging Theory*, Princeton University Press, Princeton, NJ.

Stolba, A., and Wood-Gush, D. G. M., 1980, Arousal and exploration in growing pigs in different environments, *Appl. Anim. Ethol.* 8:382–383.

Sullivan, P. F., Fifield, W., Kennedy, M., Mulder, R. T., Sellman, J. D., and Joyce, P. R., 1998, No association between novelty seeking and type 4 dopamine receptor gene (DRD4) in two New Zealand samples, *Am. J. Psychiatry* 155:98–101.

Tardiff, S., 1994, Sensitive *Saguinus* and courageous *Callithrix*: differences in adaptability and neophobia in two callitrichid genera, *Proc. Am. Zoo Ass. Reg. Conf.* 1994: 408–412.

Thorpe, W. H., 1945, The evolutionary significance of habitat selection, *J. Anim. Ecol.* 14: 67–70.

Thorpe, W. H., 1956, *Learning and Instincts in Animals.* Methuen and Co., London.

Todt, D., Hammerschmidt, K., and Hultsch, H., 1992, The behaviour of Barbary Macaques (*Macaca sylvanus*): perspective and projects of a long-term study, *Primate Report* 32: 19–27.

Torigoe, T., 1985, Comparison of object manipulation among 74 species of nonhuman primates, *Primates* 28:182–194.

Turro-Vincent, I., Launey, F., Mills, A. D., Picard, M., and Faure, J. M., 1995, Experimental and genetic influence on learnt food aversions in Japanese Quail selected for high or low levels of fearfulness, *Behov. Proc.* 34:23–41.

Vaughn, F. A., 1983, Startle responses of Blue Jays to visual stimuli presented during feeding, *Anim. Behav.* 31:385–396.

Verbeek, M. E. M., Drent, P. J., and Wiepkema, P. R., 1994, Consistent individual differences in early exploratory behaviour of male Great Tits, *Anim. Behav.* 48:1113–1121.

Verbeek, M. E. M., Boon, A., and Drent, P. J., 1996, Exploration, aggressive behaviour, and dominance in pair-wise confrontations of juvenile male Great Tits, *Behaviour* 133: 945–963.

Verbeek, M. E. M., De Geode, P., Drent, P. J., and Wiepkema, P. R., 1999, Individual behavioural characteristics and dominance in aviary groups of Great Tits. *Behaviour* 136:23–48.

Vince, M. A., 1960, Developmental changes in responsiveness in the Great Tit *Parus major, Behaviour* 15:219–242.

Visalberghi, E., and Fragaszy, D., 1995, The behaviour of Capuchin Monkeys *Cebus apella* with novel foods: the role of social context, *Anim. Behav.* 49:1081–1097.

Visalbergbi, E., Valente, M., and Fragaszy, D., 1998, Social context and consumption of unfamiliar foods by Capuchin Monkeys (*Cebus apello*) over repeated encounters, *Am. J. Primat.* 45:367–380.

Webster, S. J., and Lefebvre, L., 2000, Neophobia by the Lesser-Antillean Bullfinch, a foraging generalist, and the Bananaquit, a nectar specialist, *Wilson Bull.* 112:424–427.

Welker, W. I., 1956, Some determinants of play and exploration in Chimpanzees, *J. Comp. Physiol. Psychol.* 49:84–89.

Werner, T. K., and Sherry, T. W., 1987, Behavioral feeding specialization in *Pinaroloxias inornata*, the "Darwin's Finch" of Cocos Island, Costa Rica, *Proc. Natl. Acad. Sci.* 84:5506–5520.

West, M., 1977, Exploration and play with objects in domestic kittens, *Dev. Psychobiol.* 10: 53–57.

Wilson, D. S., 1998, Adaptive individual differences within a single population, *Phil. Trans. R. Soc. Lond. B* **353**:199–205.

Wilson, D. S., Clark, A. B., Colman, K., and Dearstyne, T., 1994, Shyness and boldness in humans and other animals, *Trends Ecol. Evol.* **9**:442–446.

Wood-Gush, D. G. M., Vestergaard, K., and Petersen, D. V., 1990, The significance of motivation and environment in the development of exploration in pigs, *Biol. Behav.* **15**:39–52.

Wünschmann, A., 1963, Quantitative Untersuchungen zum Neugierverhalten von Wirbeltieren, *Z. Tierpsychol.* **20**:80–109.

Wyles, S. J., Kunkel, J. G., and Wilson, A. C., 1983, Birds, behavior, and anatomical evolution, *Proc. Natl. Acad. Sci.* **80**:4394–4397.

Yeaton, R., and Cody, M., 1973, Competitive release in island Song Sparrow populations, *Theor. Pop. Biol.* **4**:42–58.

Zach, R., and Falls, J. B., 1976, Foraging behaviour, learning, and exploration by captive Ovenbirds (*Aves: Parulidae*), *Can. J. Zool.* **54**:1880–1893.

CHAPTER 4

AVIAN QUANTITATIVE GENETICS

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1. INTRODUCTION

Most of the characteristics studied by avian ecologists relate to the external appearance of birds—morphology, life history, behavior, and in some cases, physiology—the very characteristics upon which natural selection operates. These traits are likely to be the products of tens or hundreds of loci, and their expression can be modified by numerous environmental factors (Lynch and Walsh, 1998; Falconer and Mackay, 1996). The study of the emergent and evolutionary properties of this type of multifactorial inheritance is known as *quantitative genetics*, and it is based on indirect statistical inference rather than direct observation of specific loci and their gene products. The theory of quantitative genetics has been subject to considerable empirical scrutiny, and its successful application in plant and animal breeding testifies to its practical utility (Lynch and Walsh, 1998; Falconer and Mackay, 1996; Hill and Mackay, 1991; Mather and Jinks, 1982).

In recent years, quantitative genetic analysis and reasoning have increasingly assumed an important role in studies of adaptation and evolution in the wild (Mousseau *et al.*, 2000; Mousseau and Fox, 1998; Schlic-

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