

THE ROLE OF NEOPHOBIA AND NEOPHILIA IN THE DEVELOPMENT OF INNOVATIVE BEHAVIOUR OF BIRDS

RUSSELL GREENBERG

Why study ecological innovation?

Ecological innovation is the adoption of behaviours that allow individuals in a population to exploit newly available, previously unused, or familiar resources in a new way. Innovative behaviours have often been considered the stuff of anecdotes and short communications in natural history oriented journals. Still, in recent decades, innovative behaviour has attracted the attention of researchers investigating very different questions aimed at diverse levels of biological organization. Psychologists and ethologists have been fascinated by the origins of innovation and creativity that might result from play behaviours (Bekoff and Byers, 1998); behavioural ecologists have been documenting the way that innovative behaviours might arise and spread within social groups and through populations (Fisher and Hinde, 1949; Kummer and Goodall, 1985; Fragaszy and Visalberghi, 1990); and ecologists have been investigating how different levels of ecological flexibility develop and the implications this has for different life history strategies of related species (Morse, 1980) and their ability to colonize new places (Sol *et al.*, 2002). However, innovative behaviours have arguably gained greatest theoretical importance when related to the role they might play in rapid macro-evolutionary changes. It has been suggested that behavioural innovations that spread through populations and change the way that animals interact with their environment can eventually lead to new morphological and physiological adaptations (Mayr, 1963).

The idea that the development and spread of innovative behaviour may play a critical role in the propensity towards macroevolutionary shifts is an old one. Over 100 years ago, Lloyd Morgan (1886) argued that behavioural plasticity paved the way to major genetically based adaptations to new environments. The importance of ecological innovation in driving morphological evolution gained centre stage upon the publication of a paper by Wyles *et al.* (1983). Wyles *et al.* hypothesized that the rapid morphological evolution of birds and mammals was facilitated by the spread of new behaviours. By this hypothesis, the propensity to engage in new behaviours and the speed at which they are socially transmitted are key

factors leading to morphological change in vertebrates. This line of thinking leads to the concept of innovation-prone taxa. These taxa are bestowed with qualities that either increase the occurrence of innovative behaviour in individuals, lead individuals to replicate these behaviours within their own repertoire, or speed up or render more reliable the transmission of these behaviours between individuals and groups of individuals.

How do we study innovation?

Although the importance of innovative behaviour has long been recognized, the means to subject innovation to scientific study has proven elusive. Innovative behaviours have proven to be difficult to study within the traditional experimental paradigm of comparative psychology. Successful innovations, almost by definition, are rare events that may not occur within the confines of a particular controlled environment (see also Lefebvre and Bolhuis, Chapter 2 and Byrne, Chapter 11). Until recently, field studies of innovative behaviour have focused primarily on longitudinal studies of primate populations (Kummer and Goodall, 1985) and some prominent changes in behaviour in birds, such as the opening of milk bottles by British tits (Fisher and Hinde, 1949). For most vertebrates, it has been difficult to amass a systematic data set that would lend itself to broad comparative analysis. In the past decade, Lefebvre and his coworkers have developed an analytical technique that relies upon the publication of notes describing unusual behaviours of birds in the ornithological literature (Lefebvre *et al.*, 1997, 2001; Nicolakakis and Lefebvre, 2000; Lefebvre and Bolhuis, Chapter 2). Techniques such as these may allow us to examine the evolutionary correlates of innovative tendencies across taxa.

An alternative approach to the direct study of the occurrence of innovative behaviours is a more reductionistic focus on the behavioural syndromes that favour the acquisition and spread of innovative behaviours in populations. In this chapter I will examine the possible link between novelty responses and the probability that an innovation will arise in a particular species. The concept of innovation is inexorably wed to that of newness. In fact, the first dictionary definition of the word 'innovate' is 'the introduction of something new' (*Webster's New College Dictionary*, 1995). Therefore, it should not be surprising that the thesis of this chapter is that the response to novelty in animals plays a pivotal role in the probability that innovative behaviours will develop and spread.

This chapter will address the possible role of novelty responses in shaping innovations related to foraging in birds. However, novelty responses are widespread in vertebrates and hopefully this discussion will illuminate broader issues as well.

Can we recognize innovative behaviours?

US Justice John Paul Stevens once noted that while he could not define pornography, he knew it when he saw it. This approach also seems to describe attempts to define innovative behaviour.

Definitions of innovative behaviour are those behaviours that form a qualitative break with species- or population-typical behaviour. Although innovation can involve behaviours associated with any aspect of an animal's life from its foraging behaviour to its social

interactions, in this chapter I will focus on innovations that comprise new techniques for exploiting resources or the use of new types of resources. The use of these new resources offers a new opportunity for individuals that are colonizing new habitats or are facing competition for resources in a species-typical habitat.

Operationally, innovative behaviour has been difficult to rigorously define. By including all published accounts of unusual behaviours, Lefebvre *et al.* (1997) relied upon the judgement of fieldworkers and editors of scientific journals to determine what comprises innovation. This attempt to define innovation has broken a logjam in attempts to analyse its occurrence, but not without some conceptual problems (see also Lefebvre and Bolhuis, Chapter 2). These conceptual problems centre around the *ad hoc* and potentially anthropocentric nature of a classification based on the judgement of fieldworkers as to what constitutes a meaningful qualitative break from species-typical behaviour.

Preconditions for innovative foraging behaviour in birds

Aspects of innovation

The search for innovation prone taxa forces us to establish a framework of hypothetical preconditions for the successful development and spread of innovative behaviour. I briefly present such a framework here, emphasising where novelty responses are important.

As stated above, ecological innovative behaviours can involve both the selection of a new food resource as well as the employment of a specialized behaviour. Attempts to quantify innovative behaviour have not clearly distinguished between innovative behaviours that involve an unusual motor pattern (e.g. dropping shells from the sky) from those that involve the use of distinctly different food types (e.g. consuming blood from freshly moulted feathers of other birds), or those that involve both an unusual motor pattern applied to a new food type. These different classes of innovation may have different underlying control mechanisms and distinct implications for the further evolution of morphology and behaviour in a population or species.

Ecological plasticity and stereotypy

The phenomenon of innovation is integrally related to the concepts of ecological plasticity and stereotypy (Morse, 1980). In defining plasticity, Morse focused attention away from the ecologically static notion of generalist vs specialist, which describes the range of resources used or behaviours employed under a particular set of conditions, towards the rigidity or flexibility of behaviour in the face of changing conditions. In Morse's view, ecological generalization and specialization is a character theoretically independent of plasticity and stereotypy. For example, chickadees and certain species of tropical antbirds can be observed to be foraging primarily by searching dead curled leaves hanging in the forest understorey. During the course of observations, one could classify both as specialists. However, in the case of chickadees it is a short-term preference based on a particular pattern of prey distribution, whereas the antbirds may search dead leaves day in and day out regardless of how resource distribution might change. Although it is valuable to separate the concepts, in nature the two are probably related (i.e. plastic species tend to be generalists as well). Whereas the

specialist–generalist classification can be based on comparisons of descriptive data, plasticity vs stereotypy should be teased apart by experimental perturbation of an animals environment.

Earlier, Klopfer (1967) had made a critical distinction between perceptual and motor aspects of stereotypy and plasticity—a difference we will briefly explore here. To briefly quote Klopfer ‘an animal that responds only to narrow bands of wave lengths, for instance, would be considered perceptually more stereotyped than one responding to a wider band. On the motor side, stereotypy refers to the availability of only a small variety of movements by means of which an animal can accomplish a given act’. The distinction that Klopfer made is simple, but fundamental to our understanding of the development of innovation. I will only amend it here to emphasize that stereotyped animals may respond to only limited stimuli with a small repertoire of movements because they will not, not because they cannot. That is, the restriction may be regulated by something other than physical or perceptual abilities.

Motor vs consumer plasticity

The probability of pairing a new manoeuvre with a new resource is likely to be dependent upon the inherent plasticity of motor patterns associated with foraging, which I will refer to as *motor plasticity*. Beyond the variety of motor patterns employed, simply the quantity of complex manipulation may be important as well. Primatologists, in particular, have noted a relationship between the development of innovative feeding behaviours (including tool use), the identification of problem-solving abilities, and the quantity of physical manipulation while foraging (Clarke and Boinski, 1995; Boinski *et al.*, 2000; Day *et al.*, 2003).

As I emphasized above, ornithologists invoke the term ecological or behavioural plasticity to cover dissimilar concepts. An individual can be quite restricted in the motor patterns expressed while foraging and yet be quite catholic in its choice of what to feed upon, approach, or search. In fact, I have found that in the wood warblers that I studied, those species exhibiting the most restricted range of foraging manoeuvres tended to be those with the greatest plasticity in where they foraged and on what they fed. In fact, I would argue that consumer plasticity is a survival strategy for animals that lack a behavioural specialization to exploit particular resources. To clearly distinguish the plasticity of movement patterns from the plasticity of choice of foraging site or dietary item, I will refer to the plasticity of choice to approach foods, objects, or places as *consumer plasticity*. It is in the realm of consumer plasticity that novelty responses operate.

Solving new problems: cognition vs emotion

In most discussions, innovation-prone species are characterized by their cognitive and problem-solving abilities, as well as their tendencies to learn from conspecifics (Lefebvre and Giraldeau, 1996; Reader and Laland, 2002). As a short cut for comparisons of cognition and social learning across many taxa, relative brain size (or other more specific metrics, such as forebrain size) is often used as a surrogate for cognitive ability (Lefebvre *et al.*, 1997; Timmermans *et al.*, 2000). However, the ability to solve *new* problems, involving unfamiliar stimuli, not simply any problem, is at the core of the development of ecological

innovations. Although it has received much less attention than cognitive abilities, an animal's emotional responses to the situation surrounding a problem (apparatus in lab; microhabitat in the field) may play a decisive role in its problem-solving ability. In particular, ethologists have long recognized that emotional responses to novel situations may greatly influence an animal's apparent cognitive abilities (Scott and Fuller, 1965). The tendency to approach or try novel objects or foods will not foster the development of foraging innovations alone; it is best seen as a necessary but not sufficient condition for the development of innovations. After the initial approach to the novel situation, then trial and error learning kicks in. The animal must then be able to learn to associate the new behaviours with the particular novelty and repeat the innovative performance, incorporating the new motor pattern and consumer preference into its foraging repertoire.

The social dimension

In order for the innovation to spread between individuals and through a population, the fear of novelty must be abated and the attraction to the novelty be enhanced through social transmission. Attending to the discoveries of other, perhaps more neophilic, members of a group may reduce the onus on an individual to be exploratory. Once again, much more attention has been paid to the mode of transmission of learned behaviours than the effects of sociality on novelty responses (Reader and Lefebvre, 2001). However, by influencing the propensity to approach novel situations, social responses to novelty become a critical feature in the development of innovative behaviour.

Responses to novelty

Types of responses

The classification of responses to novelty (neotic responses: Corey, 1977) has been rather simple and initially appears straightforward. We shall see that the relationship between neophobia and neophilia is more complex than the simple definitions might imply. Neophilia is the spontaneous attraction of an animal to a food item, object, or place because it is novel. Neophobia is the aversion that an animal displays towards approaching a food item, object, or place simply because it is novel. The hallmark of both responses is that although various intrinsic features of objects seem to influence the intensity of the neotic response, the response is differentially directed at new objects or stimulus and wanes with repeated exposure to the object. Among the features that contribute to the variation in the initial neotic response are stimulus complexity and the degree of discontinuity from the familiar background objects (Thorpe, 1956).

Neophobia

Fear of novelty or preference for the familiar?

A common response of birds to new foods or objects is to display signs of fear, for instance pileal erection, displacement behaviours, and 'jumping jacks', where approaches are punctuated by short backwards hops (Coppinger, 1969; Greenberg, 1983; Heinrich, 1988;

Beissinger *et al.*, 1994; Raudensush and Frank, 1999). However, the term neophobia is often used interchangeably to refer to (1) the mere preference for feeding on or visiting familiar foods, objects, or places and (2) the aversion or fear demonstrated to the same novel stimuli. The distinction has ramifications both for the way in which neophobia is detected and the role that it might play in the development of innovative behaviour. Lack of attention to novel stimuli suggests that novel foods or sites may be avoided because they are not recognized. An active aversion, on the other hand, indicates that the object is engendering the attention of an animal, but that habituation of the fear response is required for further exploration and learning to occur. Experimentally, neophobia is often inferred in choice tests between familiar and novel foods or sites where the animal prefers the familiar entity. However, such a preference may not reflect aversion or any other emotional response to the novel object. So an assessment of the response of an animal to a novel object presented singly, without a familiar choice, is probably more likely to elucidate an emotional response to the object. The relationship between aversion and preference may be more complicated than has generally been thought. For example, it has been suggested that after the initial neophobia is disengaged, that birds may continue to show a systematic preference for familiar foods in a process that Marples and Kelley (1999) have named 'dietary conservatism'. Furthermore, as I will discuss below, neophobia and neophilia can be displayed simultaneously and their joint intensity may signal the degree of overall attentiveness to novelty.

Testing for neophobia

In many adult birds, the response to a novel object is seemingly passive. The bird remains at a distance from the object with no obvious behavioural response. Occasionally birds make short exploratory forays to the object. However, without detailed physiological monitoring (heart rate, corticosteroids, etc.) it would be difficult to infer that the bird is showing any emotional response to novelty. One experimental strategy that has been employed for captive birds to detect the strength of neophobia is to place the object next to a familiar and preferred food and measure the increased latency to feed in the presence of the object. These types of experiments ('go/no go' experiments) have been employed for a number of taxa (ducks, tits, warblers, parrots, etc.); these studies will be discussed subsequently.

Although a neophobic response can be measured using these approaches, they only allow an assessment of the relative expression of neophobia (i.e. the latency is greater or lesser for different objects). A rarely asked question is what is the absolute effect of neophobia on the ecology of a species in the wild? In other words, how does a difference in seconds or minutes in latency translate into the probability that a novel object will be visited in the wild? The other question is the degree to which initial neophobia explains preferences for familiar foods or objects. In fact, in the go/no go experiments on neophobia, once a novel object is visited for feeding the subsequent latency to feed is low. The object is treated as if it is familiar. As mentioned before, when offered a choice between familiar and novel foods, biases against novelty may persist beyond the period of initial neophobia (Marples and Kelley, 1999). This has led to the suggestion that initial neophobia itself does not have a meaningful long-term impact on consumer choice in birds. However, feeding experiments, even those conducted in the field, are generally designed to essentially force an

interaction between bird and novelty that may not occur in nature if the initial response of a bird to novelty is passive avoidance. When birds are making hundreds or thousands of foraging decisions in a day, familiarization to novelty may not occur unless there is a behavioural catalyst that is equivalent to confining a bird to a closed space with novel objects and food.

Intrinsic vs functional neophobia

Tests for neophobia in birds have often been conducted in the wild or on wild-caught birds. The individuals in these experiments may have had distinctly different prior experiences. Although relatively uncontrolled for prior experience, these tests provide information on how individuals vary in their approach to novelty under a natural regime of behavioural development. I refer to this aspect of novelty responses as *functional neophobia*. Experiments with captive-raised individuals can allow for more careful control of the objects experienced in the life of the subject prior to the actual neophobia trials. By raising individuals of different species in similar conditions and then testing for neophobia we can assess differences in *intrinsic neophobia*. The use of the term intrinsic is a shorthand expression for neophobia measured under controlled rearing conditions. It is not meant to imply that all potential environmental or maternal effects can be eliminated. For example, these experiments generally simplify as well as control the rearing environment. Adaptive differences in neophobia may result from complex ontogenetic interactions with the environment that are eliminated in the captive environment. Therefore, we need to develop ways of integrating highly controlled laboratory and field approaches to understand the mechanisms that underlie differences in neophobia—a topic I will return to below.

Functions of neophobia

Neophobia appears to be generally present in all species of mammals and birds, and perhaps many other vertebrates as well (Corey, 1977). This suggests that neophobic responses must have a very general function that serves a wide range of animal taxa. Far less attention has been paid to variation in neophobia, yet any hypothesis that attempts to explain the role of neophobia in innovation-prone taxa would have to make robust predictions about what factors affect the different levels of its expression.

In general, a differential response to novelty is not based on specific cost and benefits ascertained by an animal, but rather the uncertainty of either the costs or benefits of approaching a novel object. Two theories have been proposed to explain the underlying adaptive advantage for neophobia and the variation in the expression of this trait: the neophobia threshold hypothesis (NTH) and the dangerous niche hypothesis (DNH). I will discuss the hypotheses and how they relate to the innovation-prone behaviour patterns.

The neophobia threshold hypothesis

The NTH provides the clearest link between variation in neophobia and ecological plasticity. The hypothesis posits that the degree of aversion to novelty plays a key role in the probability that a new resource will be investigated and hence incorporated into the niche of an adult bird. More specialized birds will remain so because of a higher level of neophobia,

and reduced neophobia should be the hallmark of generalists. By this hypothesis, intrinsic levels of neophobia are largely genetically determined and subject to natural selection. Therefore, neophobia can readily evolve in different populations or strains of species or between different species. It is important to note that this hypothesis addresses the proximate regulation of ecological plasticity. By this hypothesis, the ultimate factors that select for neophobia are those that select for specialization. Although ecologically plastic (non-neophobic) birds are free to explore and discover new resources, such exploration might be wasteful in a bird that is specialized on productive and predictable resources. The hypothesis posits that a period of juvenile exploration determines the familiar world for an individual bird and that in later life neophobia determines the probability that an individual will incorporate new objects or food, in a similar manner to the way that preferences develop in filial imprinting (Bateson, 1971). Stronger adult neophobia would act to protect preferences acquired during the juvenile period. There is good empirical support for aspects of the hypothesis. Intrinsic differences in neophobia have been established between various closely related species and strains of species, particularly domesticated vs wild forms (Barnett, 1958; DesForges and Wood-Gush, 1975; Barnett and Cowan, 1976; Mitchell, 1976; Jones, 1986). Particularly instructive are the experiments of Drent *et al.* (2003) and Dingemanse *et al.* (2002) where selection experiments led to two distinct groups of Great Tits that differed in their exploratory tendencies in a few generations. Tests that quantified exploratory tendencies included the rate of exploration of an unfamiliar room and the approach to a novel object in a familiar room, thereby encompassing novelty responses at two scales.

Comparing neophobia in ecologically plastic vs stereotypic species

The prediction that ecologically plastic species are less neophobic than related specialists has been tested only a few times. In a series of experiments on warblers in the genus *Dendroica*, Greenberg (1983, 1984a) determined that the more ecologically plastic Bay-breasted Warbler (*Dendroica castanea*) was consistently less neophobic than its more specialised congener the Chestnut-sided Warbler (*Dendroica pensylvanica*). Relevant to the topic of innovations, Greenberg (1984b) provides a number of examples of unusual foraging behaviour in the former, but not the latter species. For example, Bay-breasted Warblers appear to learn that lights (particularly ultra-violet lights) attract large number of insects, and they were observed concentrating their foraging around lights. The neophobia experiments were conducted on young ones of the year, collected during their first migration, but by no means naïve. Although long-term experiments with hand-raised Chestnut-sided Warblers showed that what was explored during the juvenile exploratory period was treated as familiar in 3- and 6-month-old birds (which would normally be on their tropical wintering grounds; Greenberg, 1984a), no such experiments were conducted on Bay-breasted Warblers, so the comparative level of neophobia in birds reared under controlled and similar conditions has not been tested.

Webster and Lefebvre (2000) tested feeding neophobia of a foraging specialist, the Bananaquit (*Coereba flaveola*), and the more generalized Lesser Antillean Bullfinch (*Loxigilla noctis*) by placing novel objects near a feeder in the wild. They found that the

dietary generalist showed a lower aversion to approaching the feeder with novel objects than did the dietary specialist. Mettke-Hoffman *et al.* (2002) conducted feeding neophobia tests on various species of captive parrots and found that the latency to feed was related to several aspects of the ecology of the species, including whether the species has an insular or continental distribution (island forms have lower neophobia) and whether the species lives in complex vs simple habitats (the latter are more neophobic). Specifically, Mettke-Hoffman *et al.* found that parrots from savannah environments are slow to approach novel objects compared to species that occupied several habitats or forest edge. They reasoned that the savannah environment was simple and predictable and hence selection to explore new resources was less intense.

In another series of captive and field experiments, Greenberg (1989, 1990a, b, 1992) tested the NTH as it might apply to two species of North American sparrows in the genus *Melospiza*. The prediction of the studies was that the Song Sparrow (*Melospiza melodia*), a widely distributed species that occupies a broad range of habitats and is a good colonist of islands, would be less neophobic than the Swamp Sparrow (*Melospiza georgiana*), a specialist of shrubby wetlands. In experiments using feeders in the field and presentation of novel objects at food cups in captivity, Song Sparrows were, indeed, far less neophobic, supporting the predictions of the NTH.

Intrinsic and functional neophobia revisited

In the sparrow study, further experiments were done on naïve individuals of both species reared under similar conditions. These experiments produced results opposite to those with wild-raised individuals. The intrinsic level of neophobia was much higher in the Song Sparrow. These surprising results suggest that something about the experience of young Song Sparrows in the wild results in their lower neophobia. One possible explanation is that immatures of the more ecologically plastic species have explored a more unpredictable and dangerous array of habitats. Reduced neophobia found in wild-reared birds is the result of an interaction between juvenile exploration and the environment.

Neophobia experiments were also conducted for Mallards (*Anas platyrhynchos*) and American Black Ducks (*Anas rubripes*) (Bolen *et al.*, unpublished data), with the prediction that the widely distributed, generalist Mallard would be more neophilic than its more specialized congener. Feeding neophobia experiments on groups reared with and without hens showed a clear difference in neophobia, but with Mallards being the more neophobic species. Furthermore, ducks reared in an enriched environment showed reduced neophobia to those reared in a depauperate environment.

These experiments also suggest that the intrinsic level of neophobia is greater in the more ecologically plastic species, perhaps as an adaptation to greater potential dangers in the life of a young Mallard. They further show that an enriched early experience does reduce later life neophobia. Along with the work on *Melospiza* sparrows, these experiments demonstrate that intrinsic fear of novelty measured under controlled rearing conditions may actually be greater in the ecologically more plastic species.

Although the studies are few, they begin to suggest that the more ecologically plastic species may actually have lower levels of neophobia when wild-caught birds are tested, yet

show higher intrinsic levels of neophobia. Much more comparative work on neophobia in both wild-reared and naïve captive-reared birds needs to be conducted. However, the results contrary to the NTH suggest that the alternative and more traditional view of the adaptive value of neophobia, the DNH, needs more scrutiny.

The dangerous niche hypothesis

The DNH follows from a more general view that the primary function of neophobia is to protect animals from the unknown potential dangers of new things rather than to maintain foraging specialization. A bird that encounters more novelty may require the protection of heightened caution when exploring new objects and new foods, particularly if toxic foods or a high level of threat from predators characterize its environments. This has been the classic explanation for why some foraging opportunists, such as House Sparrows, rats and ravens, show such high levels of neophobia (Barnett, 1957; Heinrich, 1988; Rana, 1989; Brunton *et al.*, 1993) or why such seemingly adaptable animals are often so difficult to trap and poison. These species explore novel choices, but do so cautiously. However, to further add to the paradox of neophobia in an ecologically plastic species, there is no evidence that rats and ravens in the wild show reduced neophobia based on their exposure and exploration of diverse habitats and niches. Our ignorance of the long-term dynamics of exploration and habituation to novelty in generalist species stems from the lack of study of these processes under natural (non-laboratory) conditions over long periods of time. The DNH would place the emphasis of the control of ecological plasticity in generalist species on some other behavioural mechanism. One possibility is that the innate templates for ecological decision-making are themselves less plastic. Increased neophilia would be another candidate. High neophilia in species displaying high protective neophobia would seem contradictory, unless neophilia and neophobia are not necessarily the ends of a single behavioural continuum, a point I will develop further below.

Neophilia

Uncurious adults

Neophilia is the attraction that an animal shows towards an object simply because it is unfamiliar. Studies of neophilia in birds are based on the speed and frequency of tendency to spontaneously approach and manipulate new objects rather than the increase in latency to approach a food source associated with a novel object. Ornithologists have reported few instances of neophilia in adult birds, particularly in wild settings. There is evidence of object exploration that is not directly related to foraging in some taxa (Ortega and Beckoff, 1987; Mettke-Hoffmann, 1999). However, the phenomenon appears to be either generally uncommon in adults of most bird species or it is masked and hard to detect.

Neophilia and neophobia: opposites or partners?

A masking of neophilia could occur because of the potentially complex interaction of neophobia and neophilia at a novel object. I began the discussion by contrasting neophobia and neophilia as opposite reactions along a potential gradient of reactions to novelty.

It would be fair to say that most ecologically based studies of novelty responses equate neophilia with the lack of neophobia and vice versa. However, the actual relationship between neophilia and neophobia is a continuing area of mystery. The commonly observed ambivalent approach-withdrawal responses can be explained by a two-factor model, which holds that neophobia and neophilia are best considered as two independent responses to a novel stimulus (Russell, 1973). A neophilic response simultaneous to an initially strong neophobic response will contribute to any habituation to a novel food or object. If the time function for habituation of neophilia and neophobia are different then a period of neophobia will be followed by a period of exploration, allowing the bird to habituate. Greenberg and Mettke-Hoffman (2001) presented a two-by-two table of the possible combinations of degree of neophobia and neophilia (Table 8.1). They noted that some of the most innovative taxa (corvids and psittacines) show strong tendencies towards both neophobia and neophilia, leading to a complex but intense reaction to novelty. The hypothesis is that these species depend upon exploring new situations to survive, but they do so with a high level of fear and arousal, thus protecting themselves in the face of the potential, unknown dangers that are associated with novelty. Furthermore, Greenberg and Mettke-Hoffman hypothesized that neophilia and neophobia are shaped by different selective factors: neophilia is related to the potential benefits of exploring for new resources and neophobia is a response to the inherent dangers from predators etc. The resulting behaviour is a dynamic balance between the two response functions associated with these behaviours. In addition to the specific nature of the response, the overall attention to novelty may be the hallmark of an innovator. It may be necessary to focus more on the intensity of novelty responses, rather than the 'sign' of the responses (e.g. attraction vs repulsion).

The young and neophilic

Although not well studied, neophilia and object exploration are well developed in fledgling and juvenile birds, as least in passerines; this period of intense exploration and neophilia could be the primary creative period in the development of foraging repertoires as stated

Table 8.1 Simple two-by-two matrix demonstrating the hypothetical relationship between neophilia and neophobia in response to general environmental variables. Based on Greenberg and Mettke-Hoffman (2001), adapted with permission.

		<i>More complex, variable, and cryptic resources</i>	
		→	
More dangerous foraging or greater competition	↓	Low neophobia Low neophilia (e.g. pigeons)	Low neophobia High neophilia (e.g. island colonists)
	↓	High neophobia Low neophilia (e.g. tropical forest specialists)	High neophobia High neophilia (e.g. corvids and some parrots)

in the NTH. For example, Heinrich (1995) reported on the intensity with which young ravens manipulated and explored novel objects. Heinrich found that the apparent attraction to particular stimulus features (in this case, shiny objects) was more readily explainable as an attraction to novel objects. Further, the attraction was greatest to those objects that showed the greatest stimulus discontinuity with the background environment, of which shininess is a prime example. The process of maturation in ravens involved a winnowing of attractive responses to a narrower range of objects that were increasingly similar to real food objects. Heinrich interpreted neophilia as an exploratory phase of a learning process. On the other hand, the same patterns can be explained by a simple diminution of neophilia along with a separate process of trial and error learning. One would like to experimentally examine the possibility that ravens can be trained to approach particular objects as adults, objects dissimilar to what is typically preferred in wild birds, but that they preferred to explore when they were young. In other words, is neophilia a phase that young birds pass through that leads to a change of behaviour (or development of innovation) in adult birds?

The interaction between the positive attraction to novelty and its inhibition through neophobia appears to be played out along a developmental time line in young birds. Object play appears to reach the apex of importance during the late stages of dependence between young and parent (Pellis, 1981) and this is the period when the transition between fledgling and adult foraging patterns occur (Davies and Green, 1976). The period of high reactivity with foreign objects was found to increase through the juvenile period, peaking at 12–15 weeks of age in Great Tits *Parus major* (Vince, 1960). It should be noted that the reactivity and lack of inhibition referred to in Vince's work was not restricted to novel objects. Reactivity to the same object (e.g. pulling a string) occurred day after day in juvenile songbirds. However, novel objects elicit the greater attention and more vigorous response of juveniles during object play. This internal inhibition (=neophobia?) increases slowly while the spontaneous attraction to novel objects declines rapidly. It is therefore during this period of high exploratory and manipulative behaviour of objects and motor plasticity that the possibility of coupling new motor patterns with a new feeding resource is the greatest. Juvenile neophilia might be considered a prime mover in the evolution of innovation-prone taxa and we might look to differences in the long-term retention of this plasticity and the resulting behaviours for behavioural bases for innovative behaviour in birds. Alternatively, this behavioural plasticity may have other intrinsic causes or functions without contributing to the development of long-term innovative behaviour in adults.

Critical to the long term significance of object play in juvenile birds is the degree to which consistent preferences are expressed in what is explored and how these relate to adult foraging preferences. I addressed this question in a study of juvenile object exploration in a specialized and generalized insectivorous songbird (Greenberg, 1987). Hand-raised nestlings of the Worm-eating Warbler (*Helmitheros vermivorus*), a tropical migrant species that specializes in probing dead curled leaves draped on understorey plants, and Carolina Chickadees (*Parus carolinensis*), a resident species with highly generalized foraging microhabitat preferences, were presented with a range of objects, both natural and artificial, to explore during the post-fledgling period. The birds were allowed to

explore and manipulate the objects, which they did actively between feeding periods. The activity was most intense 3–4 weeks after fledging. The warblers showed a high degree of consistent individual preferences for exploring the different objects, even those warblers that were reared separately. In particular, the dead curled leaves were substantially more preferred than other objects. In general the rank correlation of preference (as determined by relative number of exploratory visits) was approximately 0.9 for all of the pairwise comparisons among warblers, even those reared apart. This suggests that the birds have a rather rigid template for what attracts their attention during exploration, which is not perceptively influenced by the activity of conspecifics. In contrast, the chickadees showed no consistent preference for any objects and individuals reared apart had a particularly low correlation of preference. Generalist species may develop idiosyncratic preferences in what they explore during juvenile object play and also allows room for social influences.

Neophobia and cognition

It seems intuitively obvious that the intensity of neophobia will influence the problem-solving ability of animals and, hence, the development of innovative behaviour. Animals that shy away from unfamiliar situations are unlikely to explore the situation enough to assess the costs and benefits of a potential foraging site or dietary item. The effect of any emotional response to novelty is generally reduced in most learning experiments through the selection of study animals that show reduced neophobia or through pre-training on experimental apparatus. Seferta *et al.* (2001) addressed this issue directly in experiments where the ability to solve a learning problem in doves and pigeons was (among other things) inversely related to the neophobia displayed in the test birds. Similarly, Webster and Lefebvre (2001) found that in a comparison of simple problem solving in five species of birds in Barbados, the neophobia of individuals was strongly negatively correlated with their overall performance on the task. Furthermore, species showing the greatest innovation rate (based on the aforementioned Lefebvre *et al.* literature review) performed the best on the cognitive task.

The importance of emotionality in general, and fear of novelty in particular, in the performance of problem-solving tasks should not be of any great surprise to students of animal learning. Consider the classic experiments of artificial selection of maze-solving ability of rats (Tyron, 1940). The initial experiments demonstrated that rats could be bred for an ability to solve a maze with few errors (maze bright) and many errors (maze dull rats) in a few generations. Subsequent testing, however, showed that the strains differed in a number of behavioural traits that indicated differences in emotionality (fear in new situations) and that these differences might have accounted for much of the apparent variation in cognitive abilities (Searle, 1949). Further research indicated that the difference in maze-learning ability disappeared for rats reared in enriched environments (Cooper and Zubeck, 1958). Taken together, these results suggest that experience and reaction to novel spaces and other aspects of novelty may have been the primary factor determining maze-solving abilities.

The brain structures important in processing novelty and engendering emotional neotic responses are poorly known in birds, but such responses are processed within the Hypothalamic-limbic system in mammals (Corey, 1977). Cognitive abilities are probably

controlled in the avian forebrain, with the hyperstriatum ventrale playing an important role (Bayley, 1984; Timmermans *et al.*, 2000). The degree to which cognition and novelty responses covary reflects independent behavioural responses that originate in different neural centres acting in consort. Therefore, the degree of neophobia can be seen to be independent of, yet possibly correlated with, problem solving and innovation. Certainly the correlation between brain areas important for cognition and for neotic responses would be an important area for further research.

Social transmission of novelty responses

If neophobia is an important intervening variable in the development of problem solving and innovative behaviour, as suggested by the Webster and Lefebvre study, then social transmission of neotic responses should be a central issue in the spread of innovations through populations. The role of group living in neotic responses is complex and has received relatively little attention. Outside of the null hypothesis that sociality has no effect, we can propose a number of ways that group living can act on novelty responses. First, simply being in a group can influence the response of individuals making them more or less neophobic (Coleman and Mellgren, 1994). Second, we could imagine different individuals might show different responses to novelty that can be transmitted to the rest of the group. For example, dominance rank may influence the propensity to incur risk while foraging and risk-prone individuals may explore novelty, providing cues to which more risk averse individuals can respond.

With respect to the effect of simply being in a group, Coleman and Mellgren (1994) examined the group effect in captive Zebra Finches (*Taeniopygia guttata*) concluding that the average latency to feed at a novel feeder was reduced in a small group compared with solitary birds because the response of slower (more neophobic) individuals was improved. This suggests that more neophobic individuals attend to the behaviour of the less neophobic individuals. Working on capuchin monkeys Visalberghi *et al.* (1998) found that social facilitation speeds up the familiarization process necessary to consume new foods.

It has been hypothesized that less dominant individuals are more prone to take risks to uncover new food sources, because dominant individuals are able to displace subordinates from any resource that proves both safe and profitable (Wilson *et al.*, 1994). This has been observed for a variety of taxa (Hegner, 1985; Stahl *et al.*, 2001). The results are somewhat mixed for the few studies of the role of social dominance in shaping novelty responses. Work on corvids (Katzir, 1982, 1983; Heinrich *et al.*, 1995) showed that individuals of low to mid dominance rank were likely to initiate the approach to novel foods, spaces, or objects and were then joined by other flock members. Mettke-Hoffman *et al.* (2002), however, found no such effect in their studies of neophobia in parrots. One cautionary note must be uttered: I know of no study where neophobia was compared for individuals in and out of a social group, thus assessing the direct effect of dominant-subordinate behavioural interactions on a particular decision to approach or avoid novelty.

In one of the few studies of interspecific interactions, Greenberg (1987b) showed that highly neophobic Chestnut-sided Warblers showed no reduction in their aversion to feed

in the presence of novel objects when in the presence of Bay-breasted Warblers, their dominant and less neophobic congeners.

While this overview does not cover all the studies of sociality and novelty responses, it shows that the role of novelty is complex and critical if we are to understand the role of sociality in the spread of innovative behaviours that are derived from the approach of novel objects or situations.

Novelty responses in major vertebrate groups

The propensity towards innovative behaviour has been proposed to vary between different taxonomic groups. Wyles *et al.* (1983) argued that the rapid rate of morphological evolution in birds and mammals relates to the frequent development and rapid social dissemination of behavioural innovations in these groups. In developing their hypothesis, they emphasized higher cognitive abilities and a greater importance of social learning in mammals and birds than other vertebrates. Research on birds has suggested that variation innovation and cognition (or the development of portions of the brain related to cognition) are associated with particular taxa (Lefebvre *et al.*, 1997; Sol and Lefebvre, 2000), with groups like corvids and parrots showing the greatest tendency to display innovative behaviours. Finally, some comparative analyses suggest that even among or within closely-related species differences in the frequency of innovation can be found (Sol *et al.*, 2002).

Attention and response to novelty of one sort or another is widespread throughout the vertebrates. However, the intensity of expression of neophilia and neophobia are known to be highly variable between closely-related species and within species and hence is a highly labile trait. Therefore, if intrinsic levels of neophilia or neophobia are associated with the development of innovation, it neither appears to be a difficult trait to evolve, nor, once it does evolve, would it necessarily lead to the evolution of innovative tendencies in a large evolutionary clade. The tendency to be attracted to and explore novel objects has been found in some reptiles (Burghardt, 1998) including turtles, varanid lizards, and crocodiles (Glickman and Sroges, 1966). However, comparative details on the quantitative nature of novelty responses for different vertebrates are generally lacking. For example, I know of no studies that examine comparative neophobia in reptiles using the latency to feed in the presence of novel objects. Do non-avian or non-mammalian vertebrates respond to novelty when it affects the context of foraging and not the potential prey itself in a manner similar to birds and mammals? Do any other vertebrates approach birds and mammals in the importance that novel object exploration has in the activity budget of juveniles?

Perhaps what varies in an evolutionarily important way is the intensity and persistence of the attention to novelty as reflected both in fear and attraction. I know of no reports of the intense period of novel object exploration found in reptiles similar to that found in many juvenile birds and mammals. The intensity of activity and length of this period may vary in important ways between major groups of birds, but has not been explored systematically. A hint of this kind of variation was provided in the broad comparison (of primarily mammals) presented in the work of Glickman and Sroges (1966). These researchers used a simple assay of 'curiosity' (neophilic object exploration) that consisted of placing a

diverse set of novel objects (one at a time) in the cage of over 200 species of mammals and reptiles in-housed in zoos. Based on this they were able to develop a broadly comparative picture of the pattern of object exploration within and between major vertebrate taxa. They found little evidence of object exploration in reptiles compared with mammals, significant variation between and within major mammalian orders, and some correlation with foraging behaviour. Similar standardized assays could be done, both in the field and in captivity, for neophobia and juvenile neophilia in birds.

Novelty responses at different ecological scales

The recent flourishing of work on ecological innovation and the ecological basis of novelty responses have progressed under a general assumption that these are general attributes of particular individuals and species that cut across different spatial scales of decision-making, from the selection of diet, to the approach of specific objects and microhabitats, to the choice of habitat. However, such consistency of responses between different aspects of decision-making in animals has been questioned both for cognitive ability and risk-taking behaviour and associated socially-related temperament (Wilson *et al.*, 1994). That there really are innovation-prone taxa characterized by greater ecological plasticity is an assumption that sits well with the intuition of naturalists, but clearly needs more rigorous empirical testing. Furthermore, the degree to which attentiveness, attraction, and aversion to novelty are correlated between decisions regarding space use, object manipulation, and diet choice has rarely been addressed. The research on behavioural syndromes in Great Tits (Verbeek *et al.*, 1994, 1996), where space and object exploration appear to be correlated with each other and to social dominance, provides tantalising evidence that individuals may have a general temperament with respect to various aspects of foraging behaviour. Clearly more work along these lines on a diversity of species needs to be undertaken.

Future research

Most of the small amount of attention that has been paid to novelty responses in the development of ecological plasticity and innovation has been focused on neophobia, the dominant response of adult birds to novelty. Neophobia has the potential of providing a brake that slows down the engagement of animals with the type of new resource that generate innovative behaviour. The NTH provides a clear framework for relating differences in the intensity of neophobic responses to ecological plasticity. The hypothesis that neophobia varies adaptively is attractive because this character has been shown repeatedly to differ within and between closely related species and thus appears to be evolutionarily labile. However, the empirical evidence for relating neophobia to plasticity and, by inference to innovation, is weak and even at times contradictory. We lack a meaningful understanding of how neophobia operates in birds outside the laboratory. We also have a poor understanding of how intrinsic levels of neophobia, those that would be measured with naïve birds in a controlled environment, relates to the functional neophobia of wild birds that have experienced variable environments. Finally, few studies have looked at neophobia in

different behavioural contexts. For example, are birds that are neophobic to objects similarly neophobic to new habitats or habitat patches on one hand, or new potential dietary items on another? Finally, recent experiments have shown that intrinsic levels of neophobia may actually be much higher in seemingly more adaptable species. The adaptive significance of different levels of intrinsic neophobia could be explained by the danger (DNH) or unpredictability of the environment. Clearly, much more phenomenological and comparative work needs to be done to determine the relationship of neophobia to the development of innovative behaviour.

Second, the dynamic interaction of neophilia and neophobia in adult birds needs more research. The model that neophobia is the dominant adaptive response to novelty in wild adult birds needs to be reconsidered in light of the potential importance that neophilia and exploration have in ameliorating the effects of neophobia. In the end, what may prove to be important in relating neotic responses to innovation is the overall intensity of the response and the degree of attention that is paid to novelty, whether the initial response is purely aversive or some combination of aversion and attraction. Attention may be better studied looking at patterns of neural activity in the brain or physiological measures of emotional arousal.

An area of research that is perhaps the most promising in terms of examining the behavioural basis of innovative behaviour is the investigation of pattern and function in juvenile neophilia. This is the time period when individuals show the greatest motor plasticity associated with object exploration and play. It is also the period of greatest consumer plasticity in the form of positive attraction to novel stimuli and active object exploration. The nexus of these behavioural patterns is intriguing, but the long-term effect of behaviours expressed and objects experienced during this period is poorly known. The degree to which behaviours developed during this period can be spread to older birds in a population is also poorly known. However, on the surface it appears to be a period of potential expansion of behaviours and preferences. It would be fascinating and challenging to attempt to induce innovative behaviour by presenting unusual resources during the juvenile exploratory period to captive birds and tracking the stability of such behaviour in adults and its subsequent spread through a captive population. It would be fruitful to quantify the variation in the intensity of exploration and neophilia in this period, making carefully designed phylogenetic and ecological comparisons.

This brief review has presented reasons to believe that novelty responses probably play a key role in the expression of cognitive abilities of birds in the wild and in determining the probability that ecological innovations will develop and spread. I have been unable to provide definitive statements on what that role is, but hopefully signposts have been set out to help inspire future research in this area. Although considerable research has been conducted on neophobia and neophilia, the study of these phenomena remain at the margins of research on animal cognition in the wild. In preparing this chapter, I perused a number of recent books in the newly flowering field of cognitive ecology and failed to find any meaningful discussion of the role of novelty responses. At the very least, I can hope that novelty responses will be viewed as a meaningful piece to the understanding of the development of innovative behaviour in the future, rather than an annoying intervening variable, obscuring underlying truths.

Summary

Innovative behaviour is closely associated with the way that animals explore or avoid novel foods, objects, or places. Whereas most studies of innovative behaviour have focused on cognition and the social transmission of learned behaviours, emotionally based novelty responses are the first line of attack or defence in the response to the novelty that is often associated with innovation.

For foraging adult birds, neophobia is the most apparent response to novelty. Although neophobia is a widespread, if not universal response, of adult birds, the intensity of expression varies considerably between individuals within a species and between closely-related species. Two hypotheses account for adaptive variation in neophobia: the NTH and the DTH. The NTH focuses on the role of neophobia in regulating ecological plasticity and the latter concentrates on the protective nature of neophobia holding that neophobia is more intense in more dangerous environments. Experiments that test these hypotheses are few. Those that examine 'functional' neophobia (e.g. the neophobia found in naturally reared birds) have found support for the NTH. However, the very few experiments on intrinsic neophobia (neophobia found in birds reared in similar and controlled environments) seem to support the DTH.

Uninhibited neophilia (aka, exploration, curiosity) is commonly expressed in juvenile birds, particularly passerines. The nexus of neophilia, object play, and a high degree of motor plasticity in juveniles make this life history stage an important one to examine for the origins of innovative behaviour. It is likely that neophilia and neophobia can function simultaneously in adult birds and that initial neophobia masks any attraction to novelty. The dynamics of the two responses can generate strongly ambivalent responses characteristic of cautious generalists (such as corvids). If this is true, then perhaps it is the intensity of the attention and emotionality in the face of novelty that is the hallmark of the innovation-prone species rather than the positive or negative nature of the response. I suggest that future research on innovative behaviour should focus, in part, on the neural substrates, long-term development, and the role of social behaviour in novelty responses in more and less innovative taxa.

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