IS SOCIAL LEARNING CORRELATED WITH INNOVATION IN BIRDS?
AN INTER- AND AN INTRASPECIFIC TEST

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ABSTRACT

This thesis focuses on the relationship between innovation and social learning in the foraging context, across and within bird species, using two different sources of data: anecdotal reports from the literature, and experimental tests in the laboratory and the field. In chapter 1, I review the trends in innovation and social learning in the avian literature, and contrast them with trends in mammals, especially primates. Three main differences are found between the two classes: (1) experimental tests of social learning have produced positive results for all birds tested so far, whereas some mammals have shown no evidence of social learning, (2) more complex motor imitation has been found in all avian taxa tested up to now, but not in all mammals, and (3) social learning in foraging contexts seems to be rare in birds, if one compares them to primates and takes into account the high rate of avian innovation. Potential sources for the observed trends are discussed, and include differences between the two groups in mobility, environmental factors, morphology of food handling organs, payoffs to alternative behaviours, group structure, and territoriality. In chapter 2, I use anecdotal reports of feeding innovation and social learning in the literature to assess taxonomic trends and to study the relationship between the two traits at the interspecific level. The association between social learning and brain size is also investigated. After the confounding effects of number of species per taxon, research effort and phylogeny are removed, innovation and social learning frequencies show a weak positive association across taxa. Various measures of brain size are also correlated with social learning frequency, but this association is mainly due to the confounding effect of common ancestry. The results of these analyses are, however, subject to caution because of the low number of social learning cases in the field, their non-normal taxonomic distribution and difficulties inferring the presumed learning mechanism. In chapter 3, I investigate the relationship between innovation and social learning at the intraspecific level in captive feral pigeons (*Columba livia*). Innovation is estimated from the ability to solve an innovative foraging problem, and social learning is measured as the number of trials required to learn a foraging task from a proficient demonstrator.

Individuals who solve the innovative problem rapidly are also fast social learners, while individuals who do poorly in the problem-solving task tend to do poorly in the social learning task. Neophobia (fear of novelty) is associated with both innovation and social learning, but does not cause the positive correlation between the two traits; once the effects of neophobia are removed from the innovation and social learning data, the correlation between the two traits remains highly significant. The ecological relevance of the problem-solving task used in captivity is validated in a field study with free-living urban pigeons.

RÉSUMÉ

Cette thèse est consacrée à l'étude de la relation entre l'innovation et l'apprentissage social dans le contexte alimentaire chez les oiseaux. La relation est considérée aux niveaux inter- et intraspécifique, en utilisant deux sources de données : des cas d'innovation et d'apprentissage social publiés dans la littérature et des tests expérimentaux en laboratoire. Dans le premier chapitre, je passe en revue les tendances d'innovation et d'apprentissage social dans la littérature ornithologique, et je compare ces tendances avec celles des mammifères, en particulier les primates. Trois différences majeures sont apparentes entre les deux classes : (1) des tests expérimentaux d'apprentissage social ont produit des résultats positifs pour toutes les espèces d'oiseaux testées jusqu'à maintenant, alors que certains mammifères semblent incapables d'apprentissage social, (2) l'imitation motrice, phénomène plus complexe, a été démontrée chez toutes les espèces d'oiseaux testées jusqu'à maintenant, mais non chez tous les mammifères, et (3) l'apprentissage social dans le contexte alimentaire semble rare chez les oiseaux, si nous les comparons aux primates et prenons en considération le taux élevé d'innovation chez les oiseaux. Les sources potentielles de ces différences sont discutées, et incluent des différences entre les deux groupes en termes de mobilité, de facteurs environnementaux, de morphologie des organes manipulateurs de nourriture, de profit des comportements alimentaires alternatifs, de structure des groupes et de territorialité. Dans le chapitre 2, j'utilise les cas anecdotiques d'innovations alimentaires et d'apprentissage social publiés dans la littérature pour évaluer la variation taxonomique dans les deux traits et pour étudier la relation entre les deux traits au niveau interspécifique. L'association entre l'apprentissage social et la taille du cerveau est aussi étudiée. Après correction pour le nombre d'espèces par groupe taxonomique, l'effort de recherche et la phylogénie, les fréquences d'innovation et d'apprentissage social montrent une corrélation positive faible. Certaines mesures de la taille du cerveau sont aussi corrélées à la fréquence d'apprentissage social, mais cette association est due principalement à l'effet de la phylogénie. Les résultats de ces analyses sont cependant sujet à caution compte tenu du faible nombre de cas d'apprentissage social sur le terrain, sa distribution taxonomique non-normale et les difficultés d'inférence sur le mécanisme présumé d'apprentissage. Dans le troisième chapitre, j'étudie la relation entre l'innovation et l'apprentissage social au niveau intraspécifique chez des pigeons captifs (*Columba livia*). L'innovation est estimée par la capacité à résoudre un problème alimentaire novateur, et l'apprentissage social est mesuré par le nombre d'essai requis afin d'apprendre une tâche alimentaire d'un démonstrateur. Les individus qui résolvent le problème novateur rapidement sont aussi ceux qui apprennent rapidement d'un démonstrateur et les individus qui performent médiocrement dans le test d'innovation apprennent très lentement ou pas du tout dans le test d'apprentissage social. Le niveau de néophobie (peur de la nouveauté) des individus est associé à leurs performances dans les tests d'innovation et d'apprentissage social, mais n'est pas la cause de la corrélation positive entre les deux traits. Une fois l'effet de la néophobie enlevé des données d'innovation et d'apprentissage social, la corrélation entre les deux traits reste très significative. La validité écologique du problème novateur utilisé en captivité est vérifiée dans une étude sur le terrain avec des pigeons urbains.

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PREFACE

Authorship and Style

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Candidates have the option of including, as part of the thesis, the text of a paper submitted or to be submitted for publication, or a clearly-duplicated text of a published paper. These texts must be bound as an integral part of the thesis.

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The thesis must still conform to all other requirements of the "Guidelines for Thesis Preparation". The thesis must include: a table of contents, an abstract in English and French, an introduction which clearly states the rationale and objectives of the study, a comprehensive review of the literature and a final conclusion and summary, and a thorough bibliography or reference list.

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CONTRIBUTION OF AUTHORS

This thesis consists of three chapters, two of which are prepared as individual manuscripts for publication. Chapter 1 is co-authored with Dr. Louis Lefebvre and will be published in a book entitled *The Biology of Traditions: Models and Evidence*, edited by Fragaszy, D. and Perry, S. and published by Cambridge University Press. I collected all the social learning data on which this chapter is based, and I wrote 50% of the manuscript. For chapter 2, I collected the data, executed the statistical analyses and wrote the manuscript. Chapter 3 is co-authored with Will Goodyer (undergraduate NSERC award holder) and Dr. Louis Lefebvre, with me as first author, and will be submitted to *Animal Behaviour*. I designed all the experiments, performed the experiments in captivity, conducted the statistical analyses and wrote the manuscript. The field experiments were done by Will Goodyer, under my supervision. Dr. Lefebvre contributed to the development of the ideas presented in chapters 2 and 3 in addition to providing editorial and technical advice.

CONTRIBUTION TO ORIGINAL KNOWLEDGE

Chapter 1. This is the first comparative study on social learning in birds and mammals, and it brings forward three previously unnoticed differences between the two classes. The possibility that social learning in the field might be rare in birds is presented for the first time. This review brings forward new ideas and hypotheses to explain the apparent rarity of social learning in birds and the differences between birds and mammals.

Chapter 2. This is the first study looking at the relationship between innovation and social learning at the interspecific level in birds. The study is also original in the way it assesses taxonomic trends in social learning in birds using anecdotal reports from the literature. The relationship between social learning and brain size is also studied for the first time in birds.

Chapter 3. This is the first experimental study on the relationship between innovation and social learning in animals. It is also the first attempt to quantify and statistically remove the effect of neophobia on cognitive variables to obtain the true association between them. The study provides the first solid evidence that a correlation between two cognitive traits measured experimentally is not spuriously caused by the intervening effect of neophobia.

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GENERAL INTRODUCTION

When an animal uses a novel solution to solve an environmental or social problem, it is said to have performed a *behavioural innovation* (Lefebvre et al. 1997b; 1998; Reader & Laland 2002). For example, some house sparrows (*Passer domesticus*) in New Zealand have learned to open automatic sliding doors by flying in front of the movement sensor controlling their opening. Once the doors are opened, the sparrows can gain access to a small cafeteria where they can feed on crumbs on the tables and the floor (Breitwisch & Breitwisch 1991). The frequency with which behavioural innovations are used to solve problems can provide an interesting measure of the tendency towards an opportunist-generalist lifestyle (Lefebvre et al. 1997b). Opportunist-generalist species exploit a wide array of resources and consequently encounter novel situations more often than their conservative-specialist counterparts. They have more opportunities for behavioural innovations and can gain more from them. In short, the ability to innovate offers opportunist-generalists a way to adjust rapidly to environmental variability (Gray 1981; Sol 2002).

By definition, innovations are both rare and unusual (Lefebvre et al. 1998) and as such it is unlikely that many members of a species would acquire a new skill through the individual learning process that can often follow innovation. In addition, newly-invented behaviours can sometimes harm the innovator. For instance, a brown pelican (*Pelecanus occidentalis*) was found dead on a beach in Mexico with stingrays in its pouch (Bostic 1966). Previous to that discovery, pelicans were not known to include cartilaginous fish in their diet, so this represents a behavioural innovation. However, the tail spine of one stingray was embedded in the pelican's throat, resulting in death from choking or poisoning, providing compelling evidence that innovations can sometimes be dangerous. Because innovations are rare and risky, they impose costs on individuals; however, it is not necessary for all members of a population to innovate if new behaviours can diffuse from experienced to naïve ones. Such diffusion of new behaviours is made possible through various mechanisms of social learning and may thus reduce the costs of innovation for many individuals.

Proposed social learning mechanisms are numerous and come with many labels. Several authors have attempted to define and classify these mechanisms in the hope of achieving a consensus (see for example Pallaud 1984; Galef 1988; Whiten & Ham 1992; Byrne & Russon 1998; Webster & Fiorito 2001), but confusion still remains. However, my concern in this thesis is more with the consequences of social learning on the diffusion of behavioural innovations rather than the exact mechanisms; the debate on terminology will thus be largely ignored, and the classification and definitions proposed by Whiten and Ham (1992) and Webster and Fiorito (2001) will be adopted. These authors use the term *mimetic process* to label "all processes whereby some aspect of the behaviour of one animal, B, comes to be like that of another, A" (Whiten & Ham 1992). They then distinguish between non-social and social mimetic processes, only the latter being of interest in this case. Social mimetic processes, in which the mimicry is dependent on a social interaction between two animals, are further subdivided into two categories: social influence and social learning. Social learning is defined as a process in which an observer learns some aspect of the behavioural similarity from a demonstrator and the various social learning mechanisms can be expressed in terms of what information is learned. In *stimulus enhancement*, an observer learns from the demonstrator to what object or location it should orient its behaviour, while in *observational conditioning*, it learns to what circumstances a given behaviour should be a response to. When an animal learns some part of a motor act from another, the term *imitation* is used. Finally when an observer learns information about the goal to pursue from a demonstrator, the mechanism is labelled *goal emulation* (Whiten & Ham 1992). All four mechanisms have the potential to cause non-genetic diffusion of behaviours through populations and/or across generations, a phenomenon labelled cultural transmission (Whiten & Ham 1992). It is important to realize that these terms have many synonyms, and that they are not always used with the same meaning in the literature.

If an important function of social learning is to allow the acquisition of new skills to exploit the environment without incurring the costs associated with innovation, we would expect the two cognitive traits to be intrinsically related. The goal of my thesis is to investigate the relationship between innovation and social learning at two different levels of analysis. I use birds as the focus of all analyses, and consider innovation and social learning only in the foraging context. In chapter 1, the trends in field reports of innovation and social learning in birds are reviewed and compared with those in mammals. In chapter 2, the taxonomic distribution of innovation and social learning reports from the literature is used to study this relationship at the interspecific level. Brain size, a potential correlate of both innovation and social learning, is also considered. In chapter 3, innovation and social learning are compared at the intraspecific level, using a standard laboratory approach with pigeons. Neophobia, a variable thought to greatly influence both innovation and social learning abilities of animals, is also considered. And finally, the ecological relevance of the laboratory approach is tested in the field in urban flocks of pigeons in Montréal, examining in particular the relationship between innovation and neophobia.

CHAPTER 1: SOCIAL LEARNING AND INNOVATION IN BIRDS AND MAMMALS: TRENDS IN THE CURRENT LITERATURE

Introduction

Since the classic studies on potato- and wheat-washing in Japanese macaques (Kawai 1965), cultural transmission has often been studied in non-human animals because it represents an important precursor to human culture. This anthropocentric program has led many researchers to study primates and to focus on cognitive traits that are associated with human culture, e.g. imitation, language, tool use and theory of mind. In this perspective, the study of non-human culture has recently culminated in the demonstration that wild chimpanzees in 7 African populations show as many as 39 behavioural variants that may be attributed to culture (Whiten et al. 1999). For psychologists and anthropologists, the concern with precursors of human behaviour in the closest relatives of *Homo* is perfectly justified. For biologists, however, the evolution of cognition must be studied on a much broader and phylogenetically distant set of taxa; in comparative biology (Harvey & Pagel 1991), one of the goals is to remove phylogenetic influences from taxonomic data and to look for independent evolution of traits as adaptations to particular ecological and life history conditions.

In this chapter, we compare the origin (innovation) and diffusion (social learning) of new feeding behaviours in birds and mammals. We first discuss the suitability of birds to a comparison with mammals, we then highlight three features by which the current literature on birds appears to differ from that on mammals, and finally we propose hypotheses to explain the differences. If this literature is an unbiased estimate of real differences between birds and mammals, the differences raise important questions on the evolution of social learning and innovations. If current trends are due to research biases, the apparent differences between birds and mammals point to gaps in our knowledge that need to be filled.

Suitability of Birds for Comparative Studies

In a comparative approach centered on independent evolution, birds are a particularly interesting group for the study of social learning, innovation and cognition in general. The ancestors of modern day birds and mammals diverged more than 300 million years ago (Hedges et al. 1996). Current avian orders are thought to have appeared 100 to 150 million years ago (Hedges et al. 1996; Cooper & Penny 1997; Cracraft 2001). If similar cognitive traits are found in some mammalian and avian taxa, it is unlikely that common ancestry could be behind the similarity. The molecular relationships between modern bird taxa have been worked out for the entire class (approximately 10 000 species; Sibley & Ahlquist 1990; Sibley & Monroe 1990), so that phylogenetic confounds can be removed from any comparative study. At least seven avian taxa appear to have independently evolved large brains (figure 1.1: based on data for 737 species in Mlíkovský 1989a; 1989b; 1989c; 1990; see Nicolakakis et al. 2002 for details): (1) Piciformes (woodpeckers), (2) Bucerotiformes (hornbills), (3) Psittaciformes (parrots), (4) Strigi (owls), (5) Accipitrida and Falconida (hawks, eagles and falcons), (6) Ciconiida (herons and penguins), and (7) Passeriformes (sub-oscines and oscines, especially corvids). These taxa represent a wide range of ecological adaptations, from tropical nut-eating in parrots to nocturnal carnivory in owls, polar piscivory in penguins, insect-eating in woodpeckers and carrion-eating in corvids. Based on embryological, neuromorphological, cytoarchitectonic and cytochemical evidence, Dubbeldam (1998), Karten (1991) and Rehkämper and Zilles (1991) have underlined the similarities between the mammalian neocortex and parts of the avian telencephalon like the hyperstriatum ventrale (HV) and neostriatum (Neo). In large-brained taxa, HV and Neo are the structures that show the largest relative increase in size (Boire 1989; Rehkämper et al. 1991), just as the neocortex does in mammals (Stephan et al. 1988).

Birds occupy environments that range from polar landmasses to open seas and deserts. Ecological and life history variables thought to be associated with complex cognition (e.g. generalism, group-living, slow development) show large variation within the class Aves. There are small, rapidly-developing species like quail and large, slowly-developing species like parrots. Some birds like Florida scrub jays live in cohesive groups with individual recognition and complex communication, while species like zenaida doves are solitary feeders year-round.

Species like snail kites have specialized, conservative diets, while others are extreme opportunist-generalists, e.g. crows and gulls. Finally, birds are the most frequently and easily observed animal taxon in the wild. Their vocalizations, flight and colour make them easier to detect than many other taxa. They are also the only animal taxon for which a popular term, "birder," exists to describe the thousands of amateurs and academics who observe and report every peculiarity of their morphology, behaviour and demographics in a large array of specialized journals. The short notes from these journals are a unique data source for the study of cognition in the field (Lefebvre et al. 1997b; 1998; Nicolakakis & Lefebvre 2000; Lefebvre 2000; Nicolakakis et al. 2002; Sol et al. 2002).

Reports of innovative feeding techniques have always been an important part of the ornithological literature, particularly in countries of English tradition. In a 1956 article on novel feeding methods by wild birds, W.H. Thorpe encouraged both amateur and professional ornithologists to note "examples of the production of original or unusual actions by birds, however small the change" (Thorpe 1956). The relationship between feeding innovations and social learning has been studied in birds for over 50 years. A decade before the studies on Japanese macaques, the first widely reported case of animal culture was the description of milk bottle opening by great tits (*Parus major*) (Fisher & Hinde 1949). The innovation was first noticed in 1921 in Swaythling, a small town in southern England. By the time Fisher and Hinde published their quantitative survey, the behaviour had been reported in over 400 localities in the British Isles. Bottle opening soon became a textbook case for animal culture, although subsequent field data (Hinde & Fisher 1951), experiments in captivity (Sherry & Galef 1984; 1990; Kothbauer-Hellmann 1990), historical research (Ingram 1998) and curve-fitting analyses (Lefebvre 1995) suggest that cultural transmission may have only been one factor in the diffusion of the new behaviour. Social learning is by no means limited to the spread of new behaviours, but innovations like bottle opening are the starting points for many studies because novelty is readily noticed in the field and, in an experiment, the introduction of a new behaviour allows efficient control of alternative mechanisms. Birds are very useful for these kinds of experiments because they rely primarily on vision during feeding, and their reliance on olfactory cues that social context provides to mammals (e.g. Galef 1996) is negligible (Campbell et al. 1999). Finally, there is a very large literature on acoustic forms of social learning in birds (Janik & Slater 2002). If some acoustic and visual forms of social learning are linked (Moore 1992) and share a common neural substrate (Iacoboni et al. 1999), the body of knowledge accumulated on bird song could provide useful directions for the study of non-vocal social learning.

Differences Between Birds and Mammals

A review of the literature on avian social learning and innovation reveals three surprising trends. First, there are no avian taxa where experiments on social learning have failed, contrary to the situation in some mammals. Secondly, all attempts to show motor imitation in birds have been successful. Third, social learning in foraging contexts appears to be rare in birds, if one compares them to primates and takes into account the high rate of avian innovation. This last point raises an obvious caveat for the first two: if social learning reports concerning foraging in birds are rare, then any conclusions about trends in this small data set should be tentative, all the more so if the rarity is due to research biases. For the moment, we will assume that the literature on birds and mammals is an unbiased sample of the true state of affairs and examine the possible origin of the differences. We will return to the question of biases later on in the chapter.

Social Learning

The first trend in the avian literature is the absence of negative results. All species in which social learning tests have been attempted eventually yield positive results. Negative results are reported by some researchers, e.g. Hitchcock and Sherry (1995) on black-capped chickadees and de Perera and Guilford (1999) on pigeons. However, these are found in species where positive results have been obtained by others (chickadees: Alcock 1969b; Krebs 1973; Sherry & Galef 1984; 1990) (pigeons: Epstein 1984; Palameta & Lefebvre 1985; Alderks 1986). In the case of Hitchcock and Sherry (1995) and de Perera and

Guilford (1999), the social learning task was applied to a specialized ability, spatial memory. The trend in birds can be contrasted with that in mammals, where some species show no sign of even the simplest form of stimulus enhancement. Cattle (Veissier 1993) and horses (Baer et al. 1983; Baker & Crawford 1986; Clarke et al. 1996) yield negative results when a naive observer witnesses a conspecific demonstrator eating from a feeder identified with a visual cue. In the case of horses, the negative results have been replicated in three different laboratories. The common feature of these species is that they are grazing herbivores. They are also gregarious, a variable often assumed to favour social learning (Klopfer 1961; Reader & Lefebvre 2001). The food they specialize on is abundant and easily accessible, however, and requires extensive digestion due to its low nutritive content, but little searching and handling.

More research is needed before negative results on two species can be generalized to an entire dietary category like herbivory. Nevertheless, if the current literature is a correct estimate of broader trends, this raises the intriguing possibility that diet is a stronger selective pressure than sociality for the evolution of socially-learned foraging (Reader & Lefebvre 2001). Up to now, only the carefully-controlled study of Templeton et al. (1999) on pinyon jays and Clark's nutcracker supports the idea that social learning is more efficient in more social species, once the confounding effects of other types of learning have been accounted for. In other birds, interspecific differences in social learning parallel differences in individual learning (Sasvári 1985a; 1985b; re-analysed by Lefebvre & Giraldeau 1996), irrespective of large differences in sociality (Lefebvre et al. 1996). In primates, the frequency of social learning reports per species is uncorrelated with group size, once phylogenetic effects have been removed (Reader 2000; Reader & Lefebvre 2001).

Among birds, the closest thing to an herbivorous mammal is a goose. Contrary to horses and cattle, geese show social learning of new food types in the field (Fritz et al. 1999) and of new handling techniques in experiments conducted in captivity (Fritz et al. 2000). Granivores, another avian group whose food source is abundant (if often patchy) and easy to handle, also show social learning. Red-winged blackbirds, for example, are agricultural pests in many parts of North America because large flocks can descend on corn fields and clean out acres of grain. The studies of Mason and Reidinger (summarized by Mason 1988) have repeatedly demonstrated intra- and interspecific social learning in this species and have indeed been designed to find socially-transmissible solutions to the pest problem posed by this species. The feral pigeon is another granivore that has often been used in social learning experiments. In the field, pigeons and other Columbiformes do not use complex searching and handling techniques for food (primarily seed and its processed derivatives like bread in cities and stored grain in ports) (Murton et al. 1972; Lévesque & McNeil 1985). Several experiments do show, however, that pigeons are capable of social learning (Epstein 1984; Palameta & Lefebvre 1985; Alderks 1986). It is possible that in pre-agricultural times, seed was a much less abundant and easily-obtained food than it is today, but in the absence of at least one negative result on an avian species, we can only conclude for the moment that there is no obvious association between diet (food type abundance and complexity of searching and handling techniques) and socially-learned feeding in birds.

Imitation

The granivorous pigeon is not only capable of simple forms of social learning, but also appears capable of more complex motor imitation. Palameta (1989) has shown that observer pigeons witnessing a demonstrator either rotating a wheel or pulling a cork to reveal a seed-filled well tend to copy the technique shown by their tutor, even if the apparatus resists because it has been modified to require the opposite technique to the one previously demonstrated. Zentall and collaborators (Akins & Zentall 1996; Zentall et al. 1996; 1998) have used a more controlled procedure, the two-action method, with pigeons as well as quails. In both species, observers tend to copy the motor variant they have seen their demonstrator use previously. These results underline the second difference between birds and mammals: imitation is found in all cases where it has been tested in birds, but several studies on mammals, in particular monkeys (Visalberghi & Fragaszy 1990; Whiten & Ham 1992) have yielded negative results. Abundant foods that are easy to find and handle may provide little selective pressure for the evolution of socially-learned foraging; these foods are also unlikely to favour motor act copying of feeding techniques. Three of the six avian species that have been shown to imitate have relatively simple food handling techniques in the wild. Budgerigars (Dawson & Foss 1965) are specialist granivores, searching for patches of seeding grass in dry areas of Australia (Kavanau 1987). Pigeons are opportunistic granivores (Johnston & Janiga 1995). *Coturnix* quails eat fallen seeds and insects obtained by scratching the ground with their foot (Snow & Perrins 1998). More complex techniques are used by the three other avian species where imitation has been demonstrated, the grey parrot (Moore 1992), the Carib grackle (Lefebvre et al. 1997a) and the common starling (Campbell et al. 1999). Grey parrots are generalist feeders that eat both seeds and fruits, but also open nuts with their beak and feet (Homberger 1986). Grackles and starlings use their manipulative beak to probe for insects in the soil and can often be seen removing wrappers around food left by humans in urban environments (Louis Lefebvre, personal communication). In the six cases available, imitating birds thus show equal proportions of complex (three cases) and simple (three cases) food handling techniques.

Aside from handling techniques in the wild, two other variables could facilitate visual imitation in food-rewarded tasks: a large neural substrate for complex cognition and the presence of vocal imitation (Moore 1992). Psittaciformes (budgerigars, grey parrots) and oscines (starlings, grackles) have a relatively large HV/Neo complex (Boire 1989; Rehkämper et al. 1991) and they also learn their vocalizations through acoustic imitation. Quails and pigeons, however, show neither of these conditions; their vocalizations are developmentally canalized and their HV/Neo complex is relatively small (Boire 1989; Rehkämper et al. 1991). Work on other species is obviously needed to reconcile these contradictory results. One key taxon where imitation research should be directed is hummingbirds (Trochiliformes). With Psittaciformes and oscines, they are the third avian taxon where acoustic imitation has been demonstrated, and this imitation ability seems to be based on neural substrates that are strikingly analogous to those of oscines (Gahr 2000; Jarvis et al. 2000). Hummingbirds are also the only taxon where there is a major discrepancy (Timmermans et al. 2000) between feeding innovation rate (high) and relative size of the HV/Neo complex (small). The presence of acoustic imitation, innovative feeding and stimulus forms of social learning (Altshuler & Nunn 2001) would all suggest that visual imitation may be found in hummingbirds. On the other hand, the relatively small size of the HV/Neo complex and the specialized nectar-probing on flowers whose shape has co-evolved with that of the beak and tongue of the bird would not favour imitative learning.

Innovations

Innovations in birds have been extensively studied in our lab for the past few years (Lefebvre et al. 1997b; 1998; Nicolakakis & Lefebvre 2000; Lefebvre 2000). We collected anecdotal reports of feeding innovations in the short notes sections of ornithological journals, and found that the frequency of feeding innovations per taxonomic group is positively correlated with relative size of the telencephalon, in particular with that of structures that are analogous to the mammalian neocortex, the hyperstriatum ventrale and the neostriatum (Timmermans et al. 2000). Reader and Laland (2002) have found a similar relationship in primates; in this order, innovation frequency per species is correlated with relative size of the neocortex and striatum. The fact that analogous neural structures are correlated with similar cognitive traits in such distant taxa as birds and primates is powerful evidence for repeated independent evolution. We could consequently expect that other correlates of innovative behaviour would be similar in birds and primates, especially if diffusion of rare, innovative behaviours is an important outcome of social learning in the two taxa. This appears not to be the case. If one looks at the relative frequencies of innovation and social learning reports in the two groups, primates and birds show different trends. In a review of the primate literature (234 species), Reader and Laland (2002) gathered a total of 558 cases of innovation and 451 cases of social learning. Of these, roughly equal numbers were field anecdotes on feeding innovations (n = 142) and on socially-learned foraging (n = 153). In birds (approximately 10 000 species), innovations seem to outnumber social learning reports. Only 67 anecdotal cases of social learning in the wild were found in the literature (appendix 1; see chapter 2 for details), compared to the 1947 feeding innovation reports currently gathered by Lefebvre and colleagues (Lefebvre et al. 1997b; 1998; Timmermans et al. 2000; Nicolakakis & Lefebvre 2000; Lefebvre 2000; Nicolakakis et al. 2002; Sol et al. 2002). Moreover, the innovation review covers a shorter time period (1970 to the present in the more important zones) and a more restricted geographical area (6 zones of the world) than the social learning survey (1949 to the present; worldwide). What these relative numbers seem to suggest is that a feeding innovation does not as readily spread to others in birds as it does in primates.

Why Do Birds and Mammals Differ?

Are the differences due to research biases and low sampling? The differences between primates and birds could reflect real trends or they could be a result of research and publication biases. For example, researchers and journal editors may expect more social learning in primates because of phyletic proximity to humans, large brains and extensive social relationships. On the other hand, anecdotal reports of the type used in innovation analysis are often criticized in psychology and primatology (see the open peer review following Byrne & Whiten 1988). This could decrease the probability that primate innovations will be noticed, written up and/or published. In contrast, short notes on new ranging, feeding and nesting behaviours are encouraged in ornithology. The journal *British Birds*, for example, has an eight member "Behaviour Notes Panel" specifically set up to referee these contributions. Because social learning is a technical concept that is inferred, not directly seen, and because there are many more non-academic ornithologists than there are non-academic primatologists, it might also be that birders notice unusual feeding behaviours more easily than they do cases of an abstract phenomenon like social learning (Daniel Sol, personal communication). Finally, the biases may lead to low sampling effort, which can lead to spurious trends. For example, the fact that imitation has been tested in only six avian species may have created a false positive, negative findings eventually emerging as more species are studied.

Other arguments, however, suggest that the differences might be real. Historically, the first widely-cited modern case of social learning (Fisher & Hinde 1949) was reported in birds by researchers from a prestigious university, Cambridge. The primate equivalent, food-washing in Japanese macaques, required translation (Imanishi & Altmann 1965) to make key papers (Itani 1965) available worldwide. Historically, the search for socially-learned foraging behaviours is thus as solidly grounded, if not more so, in birds than it was in primates. Tool use, which is often cited as a covariate of social learning (van Schaik 2002; Reader 2002), was described (1901) and reported (1919; see Boswall 1977a; 1977b; 1977c) in Darwin's finches long before it was in chimpanzees (Goodall 1964). The discovery of a new tool use case in birds is as newsworthy as it is in primates, as evidenced by the publication in *Nature* of Hunt's (1996) report on leaf tools in New Caledonian crows. The large number of papers on vocal imitation in birds further suggests that interest in socially-learned behaviours is high in ornithology.

Finally, a rough estimate of research bias for field anecdotes can be obtained by counting experimental studies. If researchers are as interested in social learning as they are in innovations, the relative number of deliberate, organized studies involving experiments should be similar. In primates, this is the case: the number of social learning (n = 84) and innovation (n = 113) cases based on experimental work is roughly equal, and the number of cases based on anecdotes is also in the same order of magnitude (n = 153 for social learning, and n = 142 for innovation). In birds, the number of social learning experiments (n = 80) cannot be compared to innovation experiments as this figure is not available. However, we know that the number of social learning cases based on anecdotes (n = 67) is similar to the number of experiments. If the number of social learning experiments in birds can be inferred from the primate pattern, we would expect no more than 70 to 150 innovation anecdotes if research effort were the sole determinant of their numbers. Instead, the sample so far includes 1947 innovation anecdotes, 30 times more than expected. We will therefore tentatively assume that the differences may reflect real trends and review the possible reasons for the apparent rarity of socially-transmitted feeding innovations in birds.

Individual and Social Learning

In birds, many innovations are single events that surprise the ornithologist and may never be seen again in the originator or in birds that are within observational range of this individual. The innovation can reflect temporary opportunism and flexibility, but it may not be incorporated into the long-term repertoire of the animal if normal food types or handling techniques yield higher payoffs. The question thus becomes one of learning in general, both individual and social. Payoffs (as they are conceptualized in behavioural ecology) and reinforcements (as they are conceived in psychology) associated with new vs. old foods and techniques determine the likelihood that the innovation will be repeated. If the innovation is rare because of its difficulty, it will be unlikely that others will acquire it because observers will have a low probability of seeing innovators repeat the new behaviour. Individual and social learning are thus linked. If an innovation has a higher probability of being incorporated into the long-term repertoire of the originator in primates than it does in birds, this alone could lead to differences in social learning trends. On average, most birds are more mobile than primates; this mobility in itself may decrease the probability of repeating an innovative behaviour done in a particular place and context.

Environmental Factors

Tebbich et al. (submitted) have recently looked at ecological variation in twig tool use by Darwin's finches in the Galapagos islands. In habitats and seasons that are extremely dry, insects withdraw into crevices to conserve water and cannot be found by gleaning on the ground. In humid habitats, gleaning is possible year-round and in this situation, Darwin's finches do not use tools, but search instead through the ground vegetation with their beaks. A similar study by Higuchi (1987) on green-backed herons documents individual differences in the use of bait-fishing in different habitats. On territories where the water is deep and herons fish from branches, lures are seldom used and individuals using them are not very successful; both lure use and success are high when water is shallow and there are many rocks and bushes for the heron to conceal itself. The studies on herons and finches suggest that birds do not use tools unless environmental conditions make alternative techniques less profitable.

Tebbich et al. (2002) have looked at the relative roles of social learning and individual practice in using twigs by finches caught in the more humid areas where they do not normally use twigs as tools. The striking result is that wild-caught finches spontaneously used twigs to feed on prey experimentally presented to them in cavities and that individual practice was as good as social learning at increasing the efficiency of birds over time. These results again underline the fact that the absence or low frequency of presumably cognitively demanding behaviours in many wild birds can reflect environmentally-determined payoffs rather than intrinsic abilities. The study by Tebbich et al. (2002) also underlines the fact that many presumably complex foraging techniques in birds may not require social learning, as Sherry and Galef (1984; 1990) and Kothbauer-Hellmann (1990) have shown for bottle opening in Paridae. An obvious point for future research in the field would be to measure the relative efficiency of simple and complex, socially-learned handling techniques in birds and primates. The usual foraging currency of nutrients per unit time should be used, as Tebbich et al. (submitted) have done for twig use and gleaning. It might very well be that, in many situations, the net energetic benefit of foods obtained through complex techniques might be lower in birds than that of foods obtained through simpler means, if only due to morphological limitations. If this is so, the cognitive potential revealed in captive studies would be less relevant than the economic variables that govern foraging decisions in the wild.

Tool Use and Morphology of Food Handling Organs

Many cases of socially-learned foraging appear to involve food types, but van Schaik (2002) has proposed that social learning and imitation may be crucial in mastering the complex motor acts required for tool use. Goal emulation may also help observers persist in improving the initial inefficiency that characterizes early attempts at tool use (Simon Reader, personal communication). If van Schaik is correct, low frequencies of social learning in birds might in part reflect the morphological limitations that make tool use (and its accompanying social learning) relatively awkward in many birds. In a review of the avian tool use literature, Lefebvre et al. (2002) found 128 cases in 108 species. This is more than some authors have expected (e.g. Thomson 1964), but the numbers are more in line with those of avian social learning (total n = 152) than they are with those of primate tool use frequency. Reader and Laland (2002) have collected 607 cases of tool use in primates, 249 of them from the wild; these numbers are in the same range as those collected for social learning and innovations.

Many avian species show frequent use of tools: leaf probes in New Caledonian crows, prey-dropping in gulls and corvids, use of rocks as shell-smashing anvils in song thrushes, use of lures to attract fish in green-backed herons. In many other cases, however, tool use is rare and seems to be used as a last resort. A case in point is Andersson's (1989) description of "egg"-breaking attempts by a fan-tailed crow in Kenya; the "egg" was a ping-pong ball and because its "shell" could not be broken, Andersson observed the entire sequence of techniques the crow had in its repertoire. The bird first tried the easiest one in terms of cognition and motor complexity, pecking at the "shell" with its beak. It then flew up with the "egg" and dropped it. When this failed, it clumsily attempted to hammer the "shell" with an oversize stone, switching at last to a stone of manageable size to increase hammering efficiency. What this example illustrates is the relative inefficiency of tool use in many avian cases. Morphological constraints may limit tool use efficiency in many birds. Birds, even flightless ones, have wings instead of arms and hands (the same limitation applies to whales and dolphins, which have flippers). True tools in birds, ones that are held directly by the animal, are moved with the beak, which is a better tool in itself than a primate hand but a poorer implement mover. Bird beaks have become morphologically specialized to crush hard shells (parrots), hammer nuts and trees (woodpeckers) and probe deep into flowers (hummingbirds) or tidal flats (shorebirds). Primate hands are in general less morphologically specialized for handling. What primate hands lack in hardness or length is made up in dexterity and in affording sight of the object during handling, two qualities that the rigid beak of birds does not have. If, as proposed by van Schaik (2002), social learning is crucial to the adoption of similar forms of tool use by members of a social group in primates, then the converse inefficiency of many tool-using birds may be one factor behind the rarity of avian social learning reports from the wild. Again, more studies of tool-using efficiency in the field are required, similar to what Tebbich et al. (submitted) have done on Darwin's finches and Zach (1979) and Cristol and Switzer (1999) have done on shell-dropping corvids.

Payoffs to Alternative Behaviours

Another factor may be differing costs and benefits of social learning and innovation across the two taxa. In behavioural ecology, the use of a behaviour by an animal in a given situation is first and foremost an economic problem, and only secondarily a question of cognitive ability. Animals that are perfectly capable of using a sophisticated ability may not do so in certain circumstances because alternative behaviours pay more. In group-living animals, payoffs are often frequency-dependent. A dramatic example of this is the effect of scrounging on social learning in pigeons. In this species, the average caged observer requires only a few demonstrations of a new feeding technique before it learns it (Palameta & Lefebvre 1985). If the naive bird is foraging with the knowledgeable one in a group, however, it can witness hundreds of demonstrations of the new technique without incorporating it in its repertoire (Giraldeau & Lefebvre 1987; Lefebvre & Helder 1997). This is because group feeding often allows animals to profit from the discoveries of others, a situation known in behavioural ecology as the producer-scrounger game (Barnard & Sibly 1981; Giraldeau & Caraco 2000). When a new technique yields a feeding payoff that can be shared, producers learn it but scroungers do not, learning instead to follow knowledgeable producers (Giraldeau & Lefebvre 1986).

Although scrounging clearly blocks learning in pigeons, its effect may not be general enough to account for the overall difference between primates and birds. First, several birds do not show the inhibitory effect of scrounging. In the field, scrub jays (Midford et al. 2000) and ravens (Fritz et al. 1997) learn even when they scrounge, while Nicol and Pope (1999) report similar results in captive chickens. Secondly, inhibitory effects of scrounging have also been reported in primates (Fragaszy & Visalberghi 1989). In Japanese macaques, adult males are also known to scrounge in situations where access to food cannot be controlled by knowledgeable individuals, e.g. wheat floating on water as opposed to potatoes held in the hand; in this situation, adult males do not learn to wash wheat, but instead take it from washing individuals (Kawai 1965).

Group Structure and Attention to Others

A fifth possibility is group structure and the way individuals in a group pay attention to the feeding behaviours of others. In many avian species, flocks are no more than aggregations, with individuals feeding in close proximity, but showing little social interactions beyond scramble competition. In pigeon flocks, for example, juveniles forage in the company of their sibling (Cole 1996) and adults in the company of their mate (Lefebvre & Henderson 1986), but interactions between unmated adults and between parents and offspring do not differ from chance (Lefebvre & Hatch, in prep.). In ringdoves, juveniles do not learn from their father more readily than they do from a familiar, but unrelated adult (Hatch & Lefebvre 1997), contrary to the parent-offspring transmission that has been suggested for social learning in Japanese macaques (Kawai 1965). Some avian species, e.g. corvids and geese, show the complex, kin-based group structure typical of primates, but many bird flocks and colonies are more similar to ungulate herds than they are to primate troops. Dunbar (1998) has proposed that the number of interactions in a group is a limiting factor for intelligence and memory and has consequently been the main selective pressure for the evolution of neocortex size in primates. The complexity of relationships in large groups is only one of the factors that are thought to select for social intelligence in primates (see Byrne & Whiten 1988; Whiten & Byrne 1997 for reviews). Differences in social learning between birds and primates could in part be due to differences in group structure and attention to others. In the only comparative study available on primates, Cambefort (1981; Jouventin et al. 1976) found that differences in social learning among vervet monkeys, mandrills and chacma baboons were indeed in the same direction as differences in gregariousness.

Territoriality

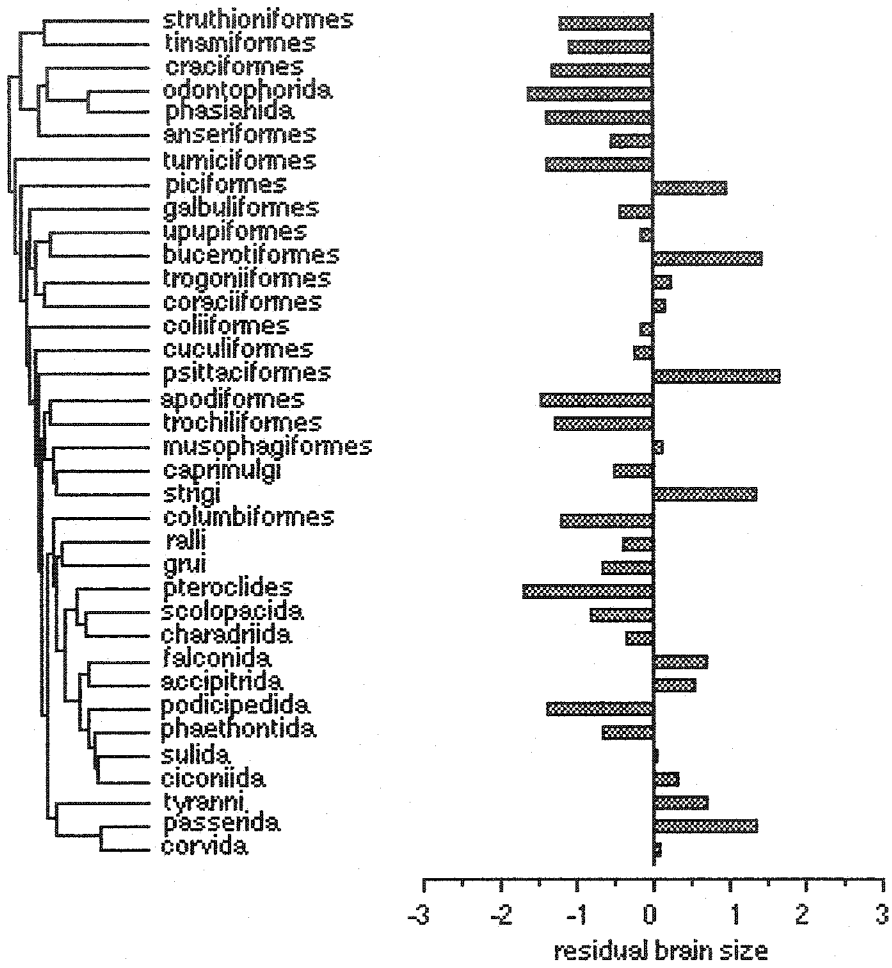
A sixth factor may be territoriality. In many species of birds, individuals defend exclusive access to a feeding area, either year-round or on a seasonal basis. Mates and fledglings may share a territory, but foraging is often solitary. In many primates, whole troops defend access to feeding ranges against other troops. Defence is still present, but does not entail solitary foraging. Members of the group can thus observe each other feeding, even if considerable spacing is often seen between individuals within a troop. Solitary foraging, combined with defence, may have obvious detrimental effects on social learning. Not only are others rarely present to provide new feeding information, but whenever they are, territorial individuals focus on aggression, not observation of foraging techniques. The limiting effects of territoriality on social learning have been demonstrated in at least three avian species. In Barbados, the zenaida dove aggressively defends year-round territories in most parts of the island, but feeds in flocks in restricted areas like the harbour, where seed spillage is available in large, temporally unpredictable patches. At the harbour, a feeding conspecific is a source of information about ephemeral patches that could be rapidly depleted by a hundred competitors or cleaned up by a human; in territorial zones, a feeding conspecific is instead an intruder that is immediately chased. Experiments have shown that territorial zenaida doves do not learn from conspecifics (Dolman et al. 1996; Lefebvre et al. 1996), but that group feeding harbour doves do (Dolman et al. 1996; Carlier & Lefebvre 1997).

Two other cases involve feeding innovations witnessed in the field. In England, blue tits have learned to pierce the base of flowers to drink the nectar. This innovation is extremely localized, however, and, contrary to milk bottle opening, has not spread to neighbouring areas or other birds (Thompson et al. 1996). The flowers bloom during a short period in the spring; foragers aggressively defend territories during this period and do not yet have fledglings to witness the behaviour and assure its vertical transmission. Thompson et al. (1996) suggest that the localized nature of the innovation may be due to these two factors. In Barbados, territorial bullfinches have also been seen to use a localized feeding innovation. At one hotel on the Caribbean coast, bullfinches pierce small paper packets of sugar and eat the contents; sugar eating is a frequent behaviour in this species, but this is usually done at open bowls. Reader et al. (2002) presented closed sugar packets at several sites along the Caribbean coast of Barbados, but saw packet opening only at the single hotel site, suggesting a localized distribution of the innovation. Territorial exclusion is the most plausible explanation for this limited transmission, intruders being chased away by residents as soon as they approach the potential learning site. Beyond these three examples, it is impossible to tell for the moment if territoriality has a general limiting effect on avian social learning.

Conclusion

Looking at the avian and mammalian (especially primate) literature on socially-transmitted feeding behaviours, we are left with a set of apparent paradoxes. Herbivorous birds like geese show social learning, contrary to herbivorous mammals like cattle and horses. Granivorous birds like budgerigars, pigeons and quails show imitation, even if they use simple food handling skills in the wild. Birds yield thousands of feeding innovation reports, but only a few dozen cases of social learning. Researchers seem to find avian social learning and imitation every time they look for it in captive experiments, but field reports are relatively rare. It is possible that these paradoxes are due to research biases and to low interest for socially-learned foraging on the part of ornithologists. More research is obviously needed to increase sample sizes on bird social learning in the foraging context and to target specific taxa. Feeding imitation should for example be studied in hummingbirds, who are already known to show stimulus forms of social learning (Altshuler & Nunn 2001). Comparative experiments on herbivorous (e.g. geese, Fritz et al. 1999; Fritz et al. 2000) vs. omnivorous (e.g. ravens, Fritz & Kotrschal 1999) species could also help us understand the role of diet in the evolution of avian social learning. Beyond these limitations in the current data set, however, it is possible that real differences exist between avian and primate social learning. Six potential sources for the differences have been discussed above, which could be compounded with basic differences in neural substrate size. Even if a crow has a much larger hyperstriatum ventrale/ neostriatum than a quail (Rehkämper et al. 1991), a primate is still much farther from the small-brained end of its class than is a corvid. A baboon has a neocortex/brainstem ratio that is 30 times the size of that of an insectivore like the tenrec (Stephan et al. 1988). The difference is even more extreme for a chimpanzee, i.e. over 50 times larger (Stephan et al. 1988). There is clearly more association area in a primate brain than in even the largest-brained bird. The combination of these neural differences with differences in mobility, group structure, territoriality, payoffs to alternatives and morphology of food handling organs could have a multiplicative effect on many cognitive traits, offering a possible explanation for the contrasting trends in primate and avian social learning.

FIGURE 1.1 Mean residual brain size (regressed against body weight) for avian orders and parvorders, based on data for 737 species in Mlíkovský (1989a; 1989b; 1989c; 1990). Phyletic tree and branch lengths based on Sibley and Ahlquist (1990).


struthioniformes
tinamiformes
craciformes
odontophorida
phasianida
anseriformes
turniciformes
piciformes
galbuliformes
upupiformes
bucerotiformes
trogoniiformes
coraciiformes
coliiformes
cuculiformes
psittaciformes
apodiformes
trochiliformes
musophagiformes
caprimulgi
strigi
columbiformes
ralli
grui
pteroclides
scolopacida
charadriida
falconida
accipitrida
podicipedida
phaethontida
sulida
ciconiida
tyranni
passerida
corvida
-3
-2
-1
0
1
2
3
residual brain size

CHAPTER 2: SOCIAL LEARNING, INNOVATION AND BRAIN SIZE IN BIRDS

Introduction

Complex cognition is often associated with large brains. The ability to innovate and learn by watching others are two of the main cognitive processes that biologists have focused on in the past decades. For example, Wyles et al. (1983) proposed that the abilities to invent and copy new behaviours are more common in species with large brains, thus allowing those species to exploit their environment in new ways and exposing them to a greater array of novel selection pressures to drive evolution. This "behavioural drive" hypothesis predicts that innovation and social learning should both be associated with large brains. If the simultaneous presence of innovation and social learning in a large-brained species has the accelerating effect on evolution envisioned by Wyles et al. (1983), this would cause a strong selective pressure for their joint occurrence at the interspecific level. Such interspecific associations between cognitive traits have been proposed as a tool for studying the possibility that animal brains are modular (Lefebvre & Bolhuis 2002). Fodor (1983; 2000) defined modules as domain-specific and autonomous computational mechanisms that are informationally encapsulated, and suggested that input systems are modular, but problem-solving abilities are controlled by general purpose processes. If limited modularity as advocated by Fodor (1983; 2000) is in fact a true reflection of brain organization, we would expect cognitive traits such as innovation and social learning to be positively correlated in two cases; either the modules they belong to have been selected together, or the traits are controlled by a general purpose cognitive mechanism. Zero correlations would be predicted if the two traits are independent and have no common evolutionary history. Finally, innovation and social learning could be negatively correlated if they are traded-off because of limits on memory and brain space (Boyd & Richerson 1985).

Using an experimental approach to investigate the relationships between innovation, social learning and brain size at the interspecific level would imply testing and comparing different species on learning and innovative problem-solving tasks. However, experimental tests of learning and problem-solving are often criticized because of the arbitrariness of the tasks chosen, the small number of species tested and the possible confounding effects of response to captivity, stimuli associated with the task and avoidance of human experimenters (Macphail 1982; Lefebvre 1996; Lefebvre et al. 1996). The taxonomic distribution of field reports of cognitive traits can be a powerful tool for comparative analysis, and an effective way around the problems associated with the experimental approach. This method is based on the assumption that the incidence of a particular cognitive ability in a species is a reflection of it's intellectual capacity (Reader & Laland 2002), and it provides a quantitative, ecologically-relevant estimate of cognition in a wide array of species. Comparative analysis of field report frequencies has been applied to deception in primates (Byrne 1993), play in mammals (Iwaniuk et al. 2001), innovation (Lefebvre et al. 1997b) and tool use in birds (Lefebvre et al. 2002), as well as social learning, innovation and tool use in primates (Reader & Laland 2002).

As predicted by the behavioural drive hypothesis, innovation frequency at the parvorder level in birds was found to be positively correlated with whole brain size (Nicolakakis et al. 2002), telencephalon size (Lefebvre et al. 1997b; Lefebvre et al. 1998; Nicolakakis & Lefebvre 2000), and size of the hyperstriatum ventrale and neostriatum (Timmermans et al. 2000). The hyperstriatum ventrale and the neostriatum are the two telencephalic structures thought to play the largest role in cognition and complex learning in birds, and are considered equivalent to the mammalian neocortex (Dubbeldam 1989; Rehkämper et al. 1991; Karten 1991; Dubbeldam 1991; 1993). In primates, both innovation and social learning frequencies at the species level are positively correlated with executive brain size (neocortex + striatum) (Reader & Laland 2002), providing further support for the predictions of the behavioural drive hypothesis. And finally, innovation and social learning frequencies are positively correlated with each other in primates (Reader & Laland 2002).

In this chapter, we look at the relationship between innovation and social learning in birds using the taxonomic distribution of field reports of both traits;

based on the results in primates, we predict a positive correlation. We also study the relationship between social learning and brain size in birds. We compare the relative size of the neostriatum and hyperstriatum ventrale with that of two other telencephalic structures that are thought to be less closely involved in cognition, the wulst and the striatopallidal complex (Karten et al. 1973; Reiner et al. 1984; Dubbeldam 1998). We predict that the neostriatum and hyperstriatum ventrale will be more closely related to social learning than the other two structures. We also look at the relationship between social learning and both whole telencephalon and whole brain sizes to increase taxonomic coverage because of the scarcity of data on specific telencephalic parts, which are only available for 32 avian species in 17 taxa (Boire 1989; Rehkämper et al. 1991).

Methods

Innovation Reports

Lefebvre and colleagues have collated field reports of innovative foraging behaviours from the short notes sections of ornithological journals for several years (see Lefebvre et al. 1997b; 1998; Nicolakakis & Lefebvre 2000 for a detailed description of the procedure). They reviewed 68 journals in six areas of the world (North America, Europe, Australia, New Zealand, India, Southern Africa) for a median time period of 30 years. A feeding innovation was defined as the incorporation of a new food type in a species diet, or the utilization of a novel foraging technique. For a report to be included, the author had to describe (or in a few cases clearly imply) the behaviour as *unusual*, *unknown*, *rare*, *opportunistic*, *adaptable*, *strange*, *not noted before*, *not recorded*. Independent readers, usually naïve to the hypothesis, showed a high level of agreement in data collection (correlations on innovation frequencies per taxon: 0.827 to 0.910, $p < 0.001$) (Lefebvre et al. 1998; Nicolakakis & Lefebvre 2000). A total of 1947 feeding innovations were found in the six zones, 541 from North America, 702 from Europe, 204 from India, 225 from Australia, 59 from New Zealand and 216 from South Africa (table 2.1). We used this collection of reports as the source of the innovation data.

Social Learning Reports

Reports of social learning in birds are much rarer than those on innovation, and differ markedly in that they often originate from experimental studies in captivity rather than simple observations in the field. In addition, the field anecdotes are rarely published in the short notes sections of ornithological journals, but mostly within full-length articles. Consequently, a systematic scanning of short notes restricted to certain parts of the world as used by Lefebvre and colleagues would not have been appropriate. In this study, we collected reports of social learning in birds in a review of the literature including both short notes and full-length articles from all parts of the world. We consulted previously published bibliographies of social learning in animals to identify avian cases (Lefebvre & Palameta 1988; Robert 1990), and found other articles likely to contain social learning reports by searching databases such as Biosis Previews and Science Citation Index and by consulting with colleagues. Finally, we reviewed the reference sections of all articles found by the three previous methods to locate similar cases. Fisher and Hinde (1949) was used as the cut-off point for modern studies; only cases published since then were considered. We adopted a broad perspective in defining social learning; all cases presumed by the authors to involve stimulus enhancement, observational conditioning, imitation and goal emulation were included. Such cases were detected by searching in the title or in the text itself for the presence of certain key words, including *social learning* and the four terms just mentioned, or any synonym or related term, i.e. learning by observation, observational learning, empathic learning, cultural transmission, social transmission, vicarious learning, learning by following, learning from a demonstrator, learning from example, local enhancement, copying, learning by watching, etc. Only reports on foraging were considered, excluding vocal learning, predator avoidance, mate choice and other non-foraging behaviours. Each social learning report encountered was classified either as having occurred in captivity or in the field, and either as an anecdotal observation or a controlled experiment. When a report mentioned several species, we credited each one with a social learning report. Species with multiple reports of the same behaviour were included only once; without this precaution, pigeons and chickens, for example, would be over-represented because of their widespread use in laboratory studies. All cases where the authors mention social learning as a possibility were included, without judgement as to whether the authors were right or wrong; this procedure was necessary to avoid subjective bias and is the same criterion used by Lefebvre et al. (1997b; 1998) and Reader and Laland (2002). An independent reader, naïve to our hypotheses, was asked to read a random sample of the literature reviewed (n = 50) and to decide whether the reports should be included or not. For included reports, the independent reader classified each report as anecdotal or experimental, and noted if it took place in the field or in captivity. The inter-judge agreement was calculated to assess the reliability of the data-gathering procedure and to ensure the objectivity of the decision-making process. The literature review uncovered a total of 152 social learning reports worldwide, among which 67 are field anecdotes, 5 are anecdotes from captivity, and 80 are experimental studies performed either in captivity or in the field (appendix 1).

Innovation and Social Learning Frequencies

Using data collected in the literature reviews, we calculated the number of foraging innovation and social learning reports per taxonomic group (table 2.1). The 35 taxa used were based on the molecular taxonomy of Sibley and Ahlquist (1990), and were chosen to follow as closely as possible the order level of classical taxonomy (as in Lefebvre et al. 1998; Timmermans et al. 2000; Nicolakakis & Lefebvre 2000). In approximately half the cases, classical orders correspond best to molecular parvorders and in the other half, to molecular orders. Sibley and Ahlquist (1990) suborders were used for three taxon (Grui, Ralli and Caprimulgi), and their molecular infraorder was used for one (Pteroclides). Nocturnal owls (suborder Strigi) were excluded from this study, as well as from the previous innovation studies, because most of their activities take place during the night and are thus difficult to detect (Lefebvre et al. 1998; Nicolakakis & Lefebvre 2000). For the rest of the chapter, the terms taxon and taxonomic group will refer to those categories as listed in table 2.1. Innovation frequencies were tabulated for each zone separately. We calculated social learning frequencies using only anecdotal reports from the field to limit the potential biases introduced by the choice of subjects in experimental studies and also by the effect of captivity. All frequencies were ln transformed (ln [x + 1]) because of the presence of numerous very small values and a few very large ones, resulting in a non-normal distribution.

Innovation and social learning frequencies were regressed against two important confounding variables, research effort and number of species per taxon (also ln transformed), to determine the most important confound of each variable. Data on research effort was obtained from Nicolakakis and Lefebvre (2000) and Lefebvre et al. (2001), and was estimated from the number of full-length papers per taxonomic group. Species number per taxon in each zone was taken from standard ornithology texts (New Zealand: Falla et al. 1979; North America: Scott 1987; India: Ali & Ripley 1995; Australia: Simpson & Day 1996; Southern Africa: Sinclair & Hockey 1996; Europe: Hagemeijer & Blair 1997). Number of species per taxon is an obvious confound that will inflate the number of observed cases in very speciose taxa. A species-rich taxon (e.g. the parvorder Passerida, 3441 species) is likely to yield more innovation and social learning reports than a species-poor one (e.g. the parvorder Odontophorida, 6 species). The number of cases found for a taxon may also be related to the interest of researchers. Thus, the confounding effect of both variables can be removed by regressing innovation and social learning frequencies against research effort or number of species; the residuals of these regressions represent measures of innovation and social learning unaffected by the confounding variables. In simple regressions forced through the origin, research effort proved to be the most important confound of innovation in five out of six zones, hence we used the studentized residuals of the innovation vs. research effort regression as the corrected innovation frequencies in the analyses presented below. These residuals were averaged over the six zones for each taxon, and weighted by the total innovation sample size its zone provided (Timmermans et al. 2000; as in Nicolakakis et al. 2002). Simple regressions forced through the origin against number of species and research effort revealed the most important confound of social learning frequencies to be number of species per taxon. We thus used the studentized residuals of the social learning vs. number of species regression as the corrected social learning frequencies in the following analyses.

Neuroanatomical Data

Although size of the hyperstriatum ventrale and neostriatum are the most important predictors of feeding innovation frequency, and also likely predictors of social learning frequency, volumetric data on specific telencephalic parts (neostriatum, hyperstriatum ventrale, striatopallidal complex and wulst) is available for only 32 species in 17 taxonomic groups (Boire 1989; Rehkämper et al. 1991). Volumetric data on whole telencephalon size is available in the literature for 140 species in 24 taxa (Portmann 1947), and data on whole brain for 767 species in 35 taxonomic groups (Mlíkovský 1989a; 1989b; 1989c; 1990). At the taxonomic levels used in this study, Timmermans et al. (2000) showed that 99.1% of the variance in hyperstriatum ventrale size can be predicted from whole telencephalon size, and Nicolakakis et al. (2002) showed that 96.2% of the variance can be predicted from the size of the whole brain. Therefore, telencephalon and whole brain sizes can be used to increase taxonomic coverage when detailed volumetric data for hyperstriatum ventrale and neostriatum is not available. For all neural measures, the size of the structure was first regressed against body weight at the genus level, and then the studentized residuals were averaged at the taxonomic levels used in this study.

Data Analyses

Non-parametric statistical procedures were used because of the non-normal distribution of the social learning residuals caused by a concentration of most reports in one taxon. Indeed, the parvorder Passerida includes 67% of all social learning field reports found in the literature. We used two sets of Spearman rank correlations to test the predicted relationships of social learning with innovation and brain size. In the first set, each taxon was entered as an independent case, without taking common ancestry into account. The second set of correlations was done on independent contrasts, to assess the potential role of common ancestry. If Passerida and Corvida both have large brains and a high innovation frequency, for example, the association between these traits could be caused by the relatively recent divergence of the two parvorders; a similar phyletic confound is less likely to be the case for Corvida and Psittaciformes, which are very distantly related. We used the CAIC computer program written by Purvis and Rambaut (1995), a technique that factors out common ancestry by estimating trait values at ancestral nodes, averaging empirical values for related extant taxa weighted by phyletic distance. The phyletic branch lengths entered in the CAIC program were taken from Sibley and Ahlquist (1990) and are based on DNA hybridization distances. The Spearman rank correlations were then performed using the contrasts, not the actual taxon used in the first set of analyses. All analyses were conducted using the SYSTAT 10.0 statistical package.

Results

Rank correlations yielded different results depending on whether phyletic corrections were used or not. Without corrections, innovation and social learning frequencies were not correlated (Spearman rho = 0.075, p = 0.669, n = 35) (figure 2.1; note that figures 2.1 to 2.6 plot the actual residuals and independent contrasts, and not the ranks used in the analyses). The neostriatum was the telencephalic structure most correlated with social learning frequency (rho = 0.500, p = 0.041, n = 17) (figure 2.2 A). Correlations with all other structures were non-significant, although by a very small margin in some cases (hyperstriatum ventrale: rho = 0.439, p = 0.078; striatopallidal complex: rho = 0.480, p = 0.051; wulst: rho = 0.331, p = 0.224; all n = 17) (figure 2.2 B-D). Social learning was also positively correlated with the size of larger neuroanatomical structures such as the telencephalon (rho = 0.441, p = 0.031, n = 24) (figure 2.3 A) and the whole brain (rho = 0.294, p = 0.087, n = 35) (figure 2.3 B), but the association with whole brain did not reach the 0.05 significance level. When phyletic corrections were applied, innovation and social learning became significantly associated (rho

= 0.398, p = 0.020, n = 34) (figure 2.4). However, the correlations with telencephalic structures were non-significant (neostriatum: rho = 0.209, p = 0.438; hyperstriatum ventrale: rho = 0.191, p = 0.478; striatopallidal complex: rho = 0.253, p = 0.345; wulst: rho = 0.012, p = 0.966; all n = 16) (figure 2.5). Larger neural structures were not significantly associated with social learning either (telencephalon: rho = 0.387, p = 0.068, n = 23; whole brain: rho = 0.182, p = 0.304, n = 34) (figure 2.6).

The data-gathering procedure for social learning reports proved to be very reliable; the principal investigator and the independent reader agreed on inclusion of reports 96% of the time, and agreed on the classification (anecdotal vs. experimental, field vs. captivity) of included reports 100% of the time.

Discussion

Three main findings emerged from our study. First, innovation and social learning in the foraging context are positively correlated across taxa in birds (figure 2.4). We estimated the taxonomic distribution of each trait from field reports, and found that variation in one trait parallels variation in the other when the confounding effects of number of species (for social learning only), research effort (for innovation only) and common ancestry were removed from the data. Secondly, size of neural substrate is positively associated with social learning frequency per taxon only before common ancestry is factored out of the data through independent contrasts (figures 2.2 & 2.3). Finally, we found that the majority of social learning field reports are concentrated in one taxon; indeed, out of the 67 field anecdotes collected, 45 (67%) are from members of the Passerida parvorder.

Reader and Laland (2002) also used comparative analysis of published field reports in primates and found a positive correlation between innovation and social learning across species. The relationship found by Reader and Laland (2002) is more robust than the one found here, because the three-way association between social learning, innovation and relative brain size holds with or without controls for common ancestry. Our data proved more sensitive to this confound, and trends varied from one version of the analyses to another. A re-analysis of Sasvári's (1985a) data on social learning in three species of tits (*Parus* spp.) and two species of thrushes (*Turdus* spp.) goes in the same direction as our finding in birds in general. When social learning scores (after reciprocal and z-score transformations to compensate for different scales of measurements) of the five species tested in Sasvári's study are compared to the feeding innovation frequencies of the same species, a positive association is found ($r = 0.525$) (figure 2.7 A), but this correlation fails to reach statistical significance with a sample size of only five ($p = 0.364$, $n = 5$). The large number of positive correlations found between innovation, learning and tool use (Lefebvre & Bolhuis 2002) seems to indicate that these cognitive traits are either controlled by a general purpose mechanism, or by different modules of cognition that share a common evolutionary history.

As predicted, one of the telencephalic areas thought to play the largest role in complex cognition, the neostriatum, yielded a higher correlation with social learning than did the striatopallidal complex and the wulst (figure 2.2). Lefebvre et al. (2002) obtained a similar result in a study of tool use in birds; the neostriatum correlated more strongly with tool use than any other telencephalic structure. What is unexpected, however, is the relatively weak correlation of the hyperstriatum ventrale with social learning, coming in third place after the striatopallidal complex. The hyperstriatum ventrale, together with the neostriatum, plays a crucial role in several kinds of learning (e.g. Horn 1990), and as thus was expected to correlate with social learning more strongly than the striatopallidal complex. This is the case for innovation; size of the hyperstriatum ventrale, followed closely by the neostriatum, is the best predictor of innovation frequency at the parvorder level (Timmermans et al. 2000). The results on telencephalic areas were confirmed at the level of the whole telencephalon, but not at the level of the whole brain (figure 2.3). Telencephalon size was significantly correlated with social learning frequency across taxa. When independent contrasts were used to remove the effect of common ancestry, however, all correlations between social learning and neural substrate size became non-significant (figures 2.5 & 2.6). This indicates that common ancestry was likely the sole cause of the observed positive associations, contrary to the situation in primates, where a positive correlation between social learning and brain size was shown to exist, irrespective of common ancestry (Reader & Laland 2002).

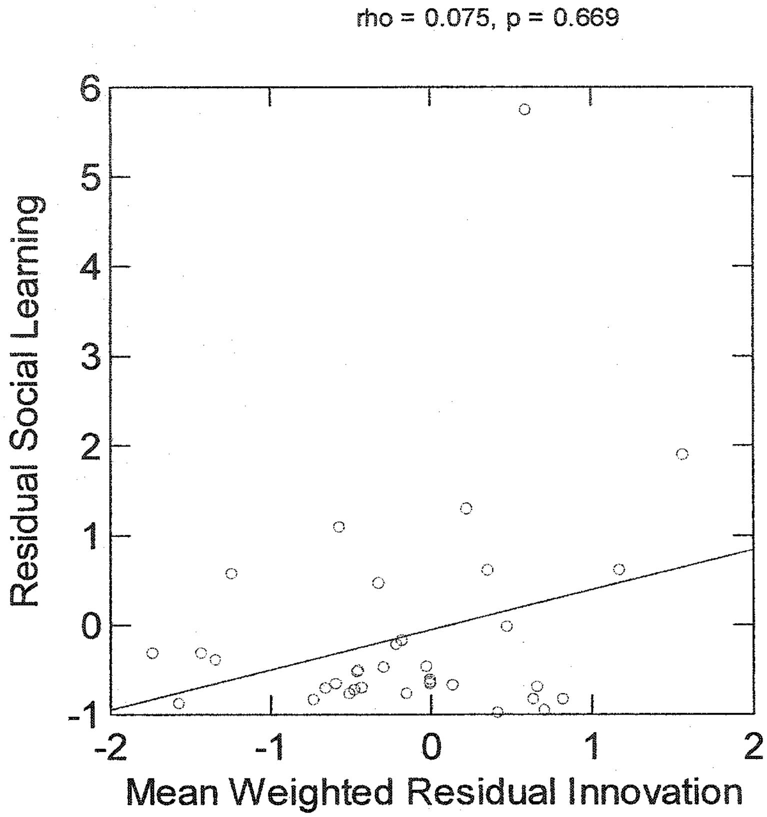
The literature review yielded 67 cases of social learning in the field, distributed among nine parvorders. The parvorder Passerida alone comprises 67% of all reports, and causes the obvious outlier in figures 2.1 to 2.3 (studentized social learning residual > 5). This much skewed distribution of social learning cases poses a problem: 26 of 35 taxa used in this study have zero social learning reports. Zero values are very difficult to interpret because it is impossible to know if they represent taxa incapable of social learning, or whether they reflect a lack of knowledge or interest about particular groups. The large number of zeros in our data set therefore introduces a large amount of uncertainty about the validity of the social learning estimate. Moreover, other problems with the data indicate that the reliability of the social learning estimate for each taxonomic group needs to be examined before any conclusions can be drawn. Contrary to innovations where anecdotes simply describe behaviours involving new foods or feeding techniques, social learning is an inferred mechanism, not an observed fact. For example, when ornithologists notice a few individuals in a familiar population performing a new behaviour, and three weeks later, a much larger number of individuals are seen using that same behaviour, they may explain the phenomenon by social learning and publish a report about it. However, such diffusion of behaviours across populations could also be explained by a variety of other factors, including asocial learning, immigration, and other ecological factors. In fact, experiments often show that anecdotal claims of social learning can in part (Sherry & Galef 1984; 1990) or in whole (Galef 1980) be attributed to other processes. Experimental reports of social learning are more reliable, but their taxonomic distribution cannot be used to estimate interspecific variation in social learning because they depend on the choice of subjects by experimenters. Also, as discussed in chapter 1, the ability to socially learn has been found in all bird species tested in captivity so far. If this means that all birds are capable of social learning, then calculating social learning frequencies from field reports becomes meaningless. Field anecdotes of social learning are therefore a very problematic data set; it is impossible to verify if their taxonomic distribution truly reflects interspecific variation in social learning, but there are serious reasons to doubt it and any definite conclusion should wait until more data are available.

TABLE 2.1 Frequency of feeding innovations and social learning reports for 35 bird taxa (NA: North America, EU: Europe, AU: Australia, NZ: New Zealand, IN: India, SA: Southern Africa, ALL: all social learning cases, FA: field anecdotes).

Taxonomic Group	Feeding Innovation						Social Learning	
	NA	EU	AU	NZ	IN	SA	ALL	FA
Accipitrida	78	66	18	4	27	47	2	1
Anseriformes	20	32	2	2	0	3	7	3
Apodiformes	3	2	2	0	1	2	0	0
Bucerotiformes	--	--	--	--	1	4	0	0
Caprimulgi	1	0	1	--	1	1	0	0
Charadriida	67	93	13	13	6	19	3	2
Ciconiida	64	46	28	3	27	32	10	0
Coliiformes	--	--	--	--	--	0	0	0
Columbiformes	0	5	4	0	2	0	12	2
Coraciiformes	2	4	6	2	12	12	0	0
Corvida	57	83	79	13	37	21	22	7
Craciformes	0	--	0	--	0	--	0	0
Cuculiformes	9	1	1	2	5	0	0	0
Falconida	22	45	14	3	0	4	0	0
Galbuliformes	--	--	--	--	--	--	0	0
Grui	5	2	2	--	1	1	0	0
Musophagiformes	--	--	--	--	--	0	0	0
Odontophorida	0	--	--	--	--	--	0	0
Passerida	137	230	20	10	58	56	75	45
Phaethontida	0	--	0	0	0	0	0	0
Phasianida	2	4	2	0	2	4	8	0
Piciformes	26	18	--	--	8	1	4	4
Podicipedida	3	7	2	0	0	1	0	0
Psittaciformes	--	--	23	0	6	0	3	1
Pteroclides	--	0	--	--	0	1	0	0
Ralli	6	20	5	1	4	4	0	0
Scolopacida	12	35	0	2	6	2	0	0
Struthioniformes	--	--	0	0	--	0	0	0
Sulida	3	9	3	2	0	1	0	0
Tinamiformes	--	--	--	--	--	--	0	0
Trochiliformes	12	--	--	--	--	--	2	0
Trogoniiformes	--	--	--	--	0	0	0	0
Turniciformes	--	--	0	--	0	0	0	0
Tyranni	12	--	0	2	0	0	4	2
Upupiformes	--	0	--	--	0	0	0	0
Total	**541**	**702**	**225**	**59**	**204**	**216**	**152**	**67**

-- denotes taxon not found in this zone

FIGURE 2.1 The relationship between residual social learning (regressed against number of species) and mean weighted residual innovation (regressed against research effort). The Spearman rho value was calculated from the ranks of the data presented in the figure.



rho = 0.075, p = 0.669

FIGURE 2.2 The relationships between residual social learning and (A) mean residual neostriatum size, (B) mean residual hyperstriatum ventrale size, (C) mean residual striatopallidal complex size, and (D) mean residual wulst size. Social learning frequencies are regressed against number of species per taxon; brain measures are regressed against body weight. The Spearman rho value was calculated from the ranks of the data presented in the figure.

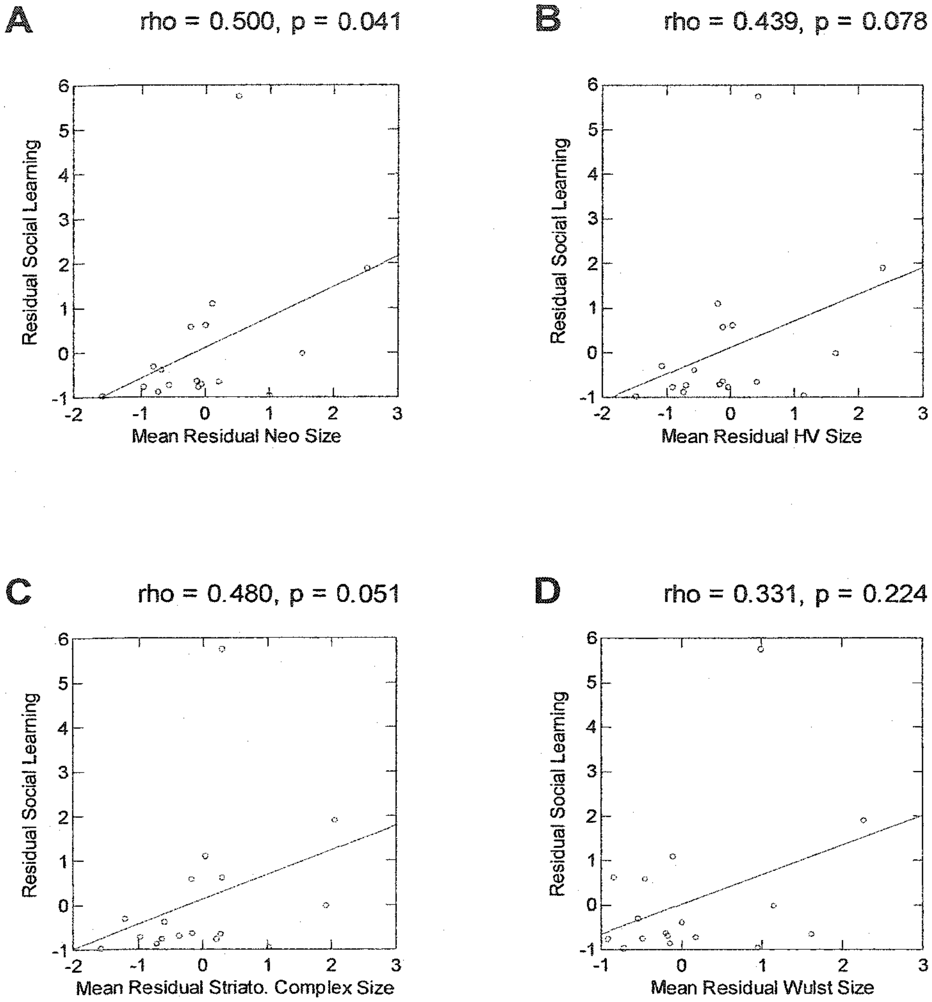
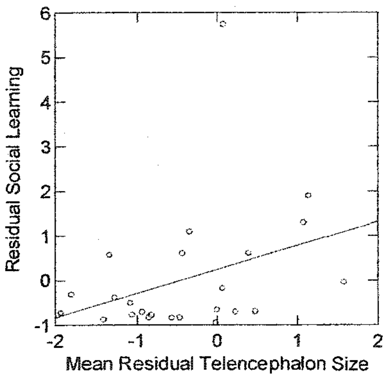

A
rho = 0.500, p = 0.041
Residual Social Learning
Mean Residual Neo Size
B
rho = 0.439, p = 0.078
Residual Social Learning
Mean Residual HV Size
C
rho = 0.480, p = 0.051
Residual Social Learning
Mean Residual Striato. Complex Size
D
rho = 0.331, p = 0.224
Residual Social Learning
Mean Residual Wulst Size
6
5
4
3
2
1
0
-1
-2
-1
0
1
2
3

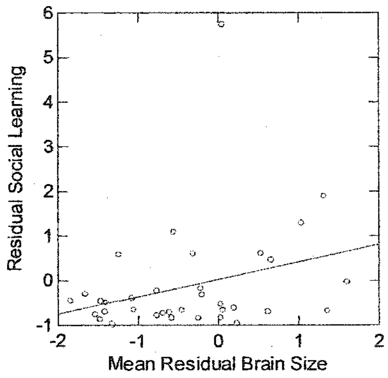
FIGURE 2.3 The relationships between residual social learning and (A) mean residual telencephalon size, (B) mean residual brain size. Social learning frequencies are regressed against number of species per taxon; brain measures are regressed against body weight. The Spearman rho value was calculated from the ranks of the data presented in the figure.

A



rho = 0.441, p = 0.031

B



rho = 0.294, p = 0.087

FIGURE 2.4 The relationship between independent contrasts of residual social learning and mean weighted residual innovation. The Spearman rho value was calculated from the ranks of the data presented in the figure.

rho = 0.398, p = 0.020

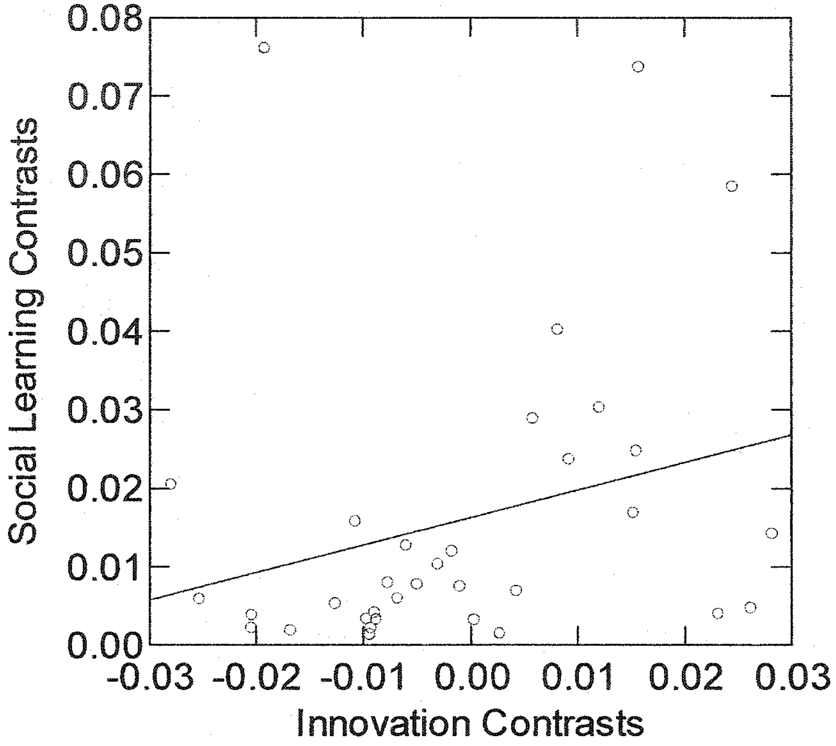
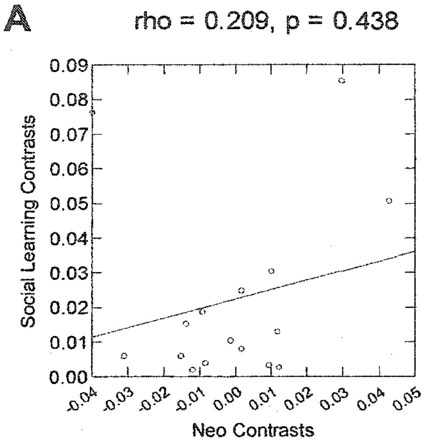
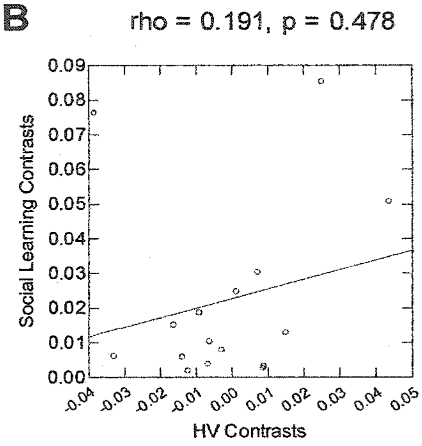
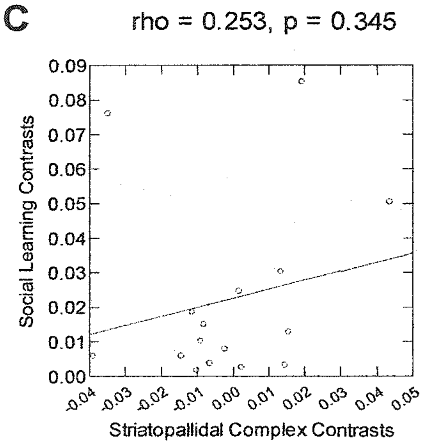


FIGURE 2.5 The relationships between independent contrasts of residual social learning and (A) mean residual neostriatum size, (B) mean residual hyperstriatum ventrale size, (C) mean residual striatopallidal complex size, and (D) mean residual wulst size. The Spearman rho value was calculated from the ranks of the data presented in the figure.


A
rho = 0.209, p = 0.438
Social Learning Contrasts
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
-0.04
-0.03
-0.02
-0.01
0.00
0.01
0.02
0.03
0.04
0.05
Neo Contrasts


B
rho = 0.191, p = 0.478
Social Learning Contrasts
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
-0.04
-0.03
-0.02
-0.01
0.00
0.01
0.02
0.03
0.04
0.05
HV Contrasts


C
rho = 0.253, p = 0.345
Social Learning Contrasts
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
-0.04
-0.03
-0.02
-0.01
0.00
0.01
0.02
0.03
0.04
0.05
Striatopallidal Complex Contrasts

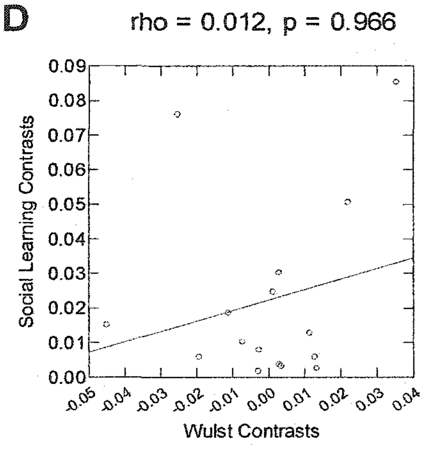

D
rho = 0.012, p = 0.966
Social Learning Contrasts
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
-0.05
-0.04
-0.03
-0.02
-0.01
0.00
0.01
0.02
0.03
0.04
Wulst Contrasts

FIGURE 2.6 The relationships between independent contrasts of residual social learning and (A) mean residual telencephalon size, (B) mean residual brain size. The Spearman rho value was calculated from the ranks of the data presented in the figure.

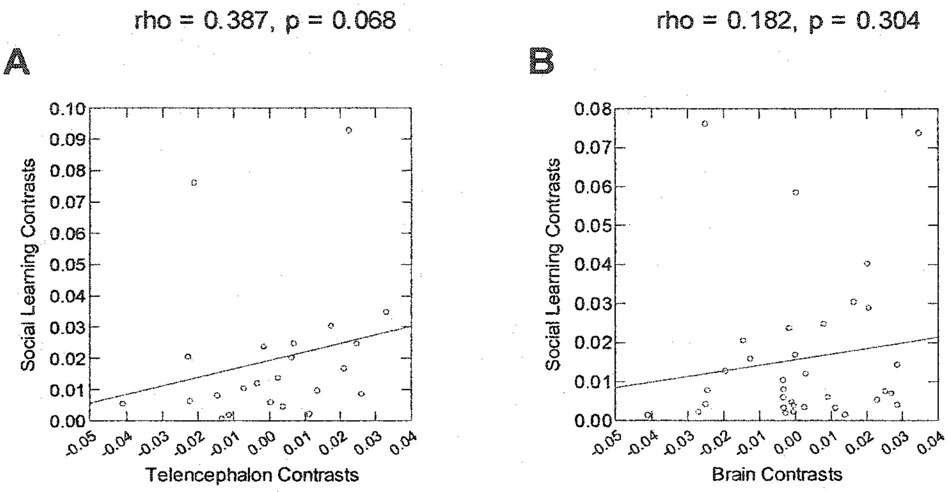
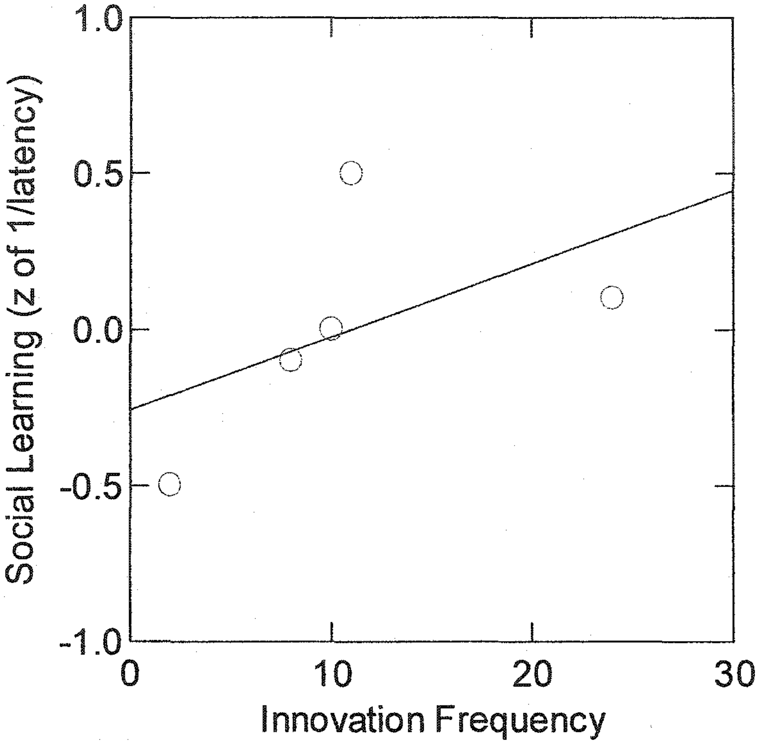

rho = 0.387, p = 0.068
A
0.10
0.09
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Social Learning Contrasts
-0.05
-0.04
-0.03
-0.02
-0.01
0.00
0.01
0.02
0.03
0.04
Telencephalon Contrasts
rho = 0.182, p = 0.304
B
0.08
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0.00
Social Learning Contrasts
-0.05
-0.04
-0.03
-0.02
-0.01
0.00
0.01
0.02
0.03
0.04
Brain Contrasts

FIGURE 2.7 The relationship between social learning speed and innovation frequency in five species of Passerida (learning data from Sasvári 1985a).

r = 0.525, p = 0.364



1.0
0.5
0.0
-0.5
-1.0
Social Learning (z of 1/latency)
0
10
20
30
Innovation Frequency

CHAPTER 3: SOCIAL LEARNING AND INNOVATION ARE CORRELATED IN PIGEONS

Introduction

Novel feeding behaviours can originate and be maintained in animal populations via two different learning mechanisms. First, an animal may ingest a new food type or invent a novel foraging technique and maintain the innovation in its repertoire through individual learning. The other possible mechanism is social learning; an individual may incorporate a novel feeding behaviour in its repertoire by watching another animal performing that behaviour. In this case, the observer does not innovate, avoiding some of the possible risks associated with novel foods or feeding techniques. The best-known examples of feeding innovations and their possible social learning are potato- and wheat-washing by Japanese macaques (*Macaca fuscata*) (Kawai 1965) and milk bottle opening by great tits (*Parus major*) (Fisher & Hinde 1949).

A number of studies have focused on social learning of feeding innovations in animal populations (see appendix 1 and chapter 2), but the relationship between the two cognitive traits has received much less attention. A notable exception is the study of Reader and Laland (2002), who looked at this relationship across species in primates, using the taxonomic distribution of innovation and social learning reports in the literature. Reader and Laland (2002) found that the frequency of innovation and social learning reports for primate species are positively correlated. In birds, the interspecific pattern is not as clear, but there seems to be no correlation between innovation and social learning (see chapter 2). Several workers have recognized the possible evolutionary consequences of the rapid, non-genetic spread of new behaviours made possible by innovation and social learning (Wyles et al. 1983; Boyd & Richerson 1985; Wilson 1985). When both traits are present in a species, new behaviours can be transmitted at a fast rate through populations, accelerating their potential effects on evolution (Wyles et al. 1983; Wilson 1985). The simultaneous presence of social learning and innovation in a species can give rise to several scenarios for the distribution of the two traits among individuals. Surprisingly, studies on these relationships at the intraspecific level are lacking. If the two traits are costly to develop and maintain, they may be traded-off and therefore negatively correlated between individuals. Another possibility is that innovation and social learning are independent processes, in which case we would expect a zero correlation. Finally, innovation and social learning may be controlled by common cognitive processes, and be positively correlated (Lefebvre & Bolhuis 2002). Such a positive correlation could also result from a common association with a third, intervening variable. In this case, the most likely candidate is neophobia (fear of novelty) (Greenberg 1983; 1984; 1990a), which can affect performance of individuals on both innovation and social learning through a common variation in fear of novel stimuli.

Although the relationship between innovation and social learning within species has not been examined yet, previous studies have looked at the intraspecific associations between related processes. For example, Webster and Lefebvre (2001) have demonstrated that innovation, as measured by performance on a novel problem-solving task, can be predicted by neophobia in five species of the West Indies, both in the field and in captivity. Individual learning and neophobia have also been shown to covary in columbids (Seferta et al. 2001). In a re-analysis of Whittle's (1996) data on two finch species, Seferta et al. (2001) found that neophobia predicts individual learning, which predicts social learning. Finally, Beauchamp et al. (1994) found a positive correlation between learning latencies of pigeons on a social and non-social task.

In this study, we tested individually caged feral pigeons (*Columba livia*) on the innovative problem-solving task developed by Webster and Lefebvre (2001), and a social learning task similar to the one used by Giraldeau and Lefebvre (1987), Giraldeau and Templeton (1991), Lefebvre and Giraldeau (1994), and Lefebvre et al. (1997a), focusing on the correlation between individual performance on the two tasks. We included a third test, neophobia, to see if an eventual positive correlation between innovation and social learning was due to a common dependence on this intervening variable. In order to insure the ecological relevance of our captive study, we also presented the innovative problem-solving and neophobia tasks to free-living, urban flocks of pigeons.

Methods

Part I – Experiments in Captivity

Subjects

Forty-four adult, wild-caught feral pigeons were obtained from a commercial dealer (Stephen Wright, Richmond Hill, Ontario). The birds were received in four different groups, one of 14, two of 12 and one group of six, over a period of six months (January to June 2001). Two birds from the first group were randomly chosen to be trained as demonstrators for the social learning test and remained in the laboratory for the whole six-month period. The remaining 42 birds (in three groups of 12 and one group of six) were subjected to a series of tests over a period of four weeks.

Experimental Procedure

Upon reception, all birds were identified with a coloured plastic leg band, and housed in single 43 x 53 x 30 cm cages. They had ad libitum access to water and grit at all times, and to a commercial seed mix for a minimum of 2 days. The birds were then weighed, and the amount of food given to them was carefully controlled on subsequent days to progressively bring all individuals down to 85-90% of their ad libitum weight for the experimental period. Once birds had reached their target deprivation weight, testing began. Before each testing day, the subjects were food deprived for 18 hours overnight, and then moved from the housing room to the experimental room where they were given a ten-minute habituation period. During all tests, the experimenter was hidden behind a blind and observed the bird's behaviour using a closed-circuit television and camera system.

We presented each subject with a series of five tests in the same order: neophobia 1, innovation, neophobia 2, social learning, and priority of access to food. Neophobia tests were performed before and after the innovation test to see whether neophobia levels would decrease after an experimental task. A gradual decrease in neophobia as testing proceeds could potentially mask any association between social learning and innovation if the order of these tests were counterbalanced or randomized. For example, if neophobia decreased throughout testing, birds tested first on innovation would do poorly on that test, and better on the social learning test; birds given the opposite order of tests would show the reverse pattern, creating a spurious negative correlation between social learning and innovation (Beauchamp et al. 1994). To alleviate this problem, tests were presented to all individuals in the same order (as in Whittle 1996; Seferta et al. 2001; Webster & Lefebvre 2001), and the level of neophobia was assessed twice.

Neophobia Tests

The neophobia tests followed the procedure designed by Greenberg (1983; 1984), and compared the latency to feed in trials randomly featuring either a novel object or no novel object (control) placed next to a food dish. The first neophobia test was conducted over three consecutive days (two trials per day, 2 h apart), with three novel object and three control trials, for a total of six trials. The second neophobia test lasted two days (two trials per day, 2 h apart), with two novel object and two control trials, for a total of four trials. Each day, we randomly determined if the novel object or the control trial would be presented first; the second trial that day then involved the opposite condition. During an experimental trial, subjects were given 20 g of mixed seeds in their usual feeding dish, and latency to initiate feeding was recorded (in seconds). If they did not feed within 20 min, the trial was ended and another trial was attempted later that day or on a subsequent day. Once the birds had fed for 5 s, the experimenter slowly approached the cage, opened the door, and placed one of five novel objects 2 cm away from the food dish. The experimenter then backed away and returned behind the blind. The latency to resume feeding after the introduction of the novel object was recorded. If an individual did not feed within 20 min, we recorded a ceiling latency of 1201 s. The novel objects were made of artificial materials and unusual man-made items to minimize the probability that they had been encountered by subjects in the past (Greenberg 1990b). The order of presentation of these objects was determined randomly, with objects 1, 2 and 3 used in the first neophobia test, and objects 4 and 5 used in the second. Control trials were conducted exactly like novel object trials, but instead of introducing a novel object, the experimenter simply put one hand in the cage for 3 s. To yield neophobia levels for each individual, latencies to feed in control trials were averaged and subtracted from mean latency to feed in novel object trials.

Innovation Test

We used the apparatus designed by Webster and Lefebvre (2001) to assess innovative problem-solving ability. A clear Plexiglas box (18 x 6.5 x 4.5 cm) (figure 3.1) was filled with the seed mix the birds were used to feed on. The box could be opened and seeds could be obtained by pulling or pushing the middle drawer, pulling the two end drawers, or removing the two lids; each lid and drawer was fitted with a metal ring (see figure 3.1). The box was placed in the centre of the birds' home cages for a single 30 min trial. We recorded the following variables: latencies to contact and open the box, number of sections of the box contacted, and number of pecks to the box (modified from Webster & Lefebvre 2001). The box was split in 13 different sections as illustrated in figure 3.1. If an individual did not open or contact the box, we recorded the ceiling latency of 1801 s.

Social Learning Test

We trained two demonstrators via shaping to remove the stopper from an inverted, opaque, test tube containing 0.5 g of mixed seeds. The stopper was fitted with a wooden tab which the pigeons could peck or grasp with the bill and twist in a downward motion to release the seeds into their food dish (see Giraldeau & Lefebvre 1987; Giraldeau & Templeton 1991; Lefebvre & Giraldeau 1994; Lefebvre et al. 1997a for other descriptions of the task). Demonstrators were considered efficient when they could routinely open the test tube in less than 5 s after presentation of the apparatus. Before the social learning test, the subjects were transferred to smaller 23 x 38 x 28 cm cages in which all sides were opaque except the door in the front. These cages had the advantage of offering very few distractions and insured that the birds were facing the door most of the time. A 20 x 5 cm hole in the door allowed the birds access to the apparatus. A control trial was performed prior to the social learning test: the apparatus was placed in front of each individual for 20 min to control for spontaneous opening.

Social learning trials were conducted over a four-day period, at the rate of five trials per day. The cages of the demonstrator and the naïve observer were placed on the floor, 40 cm apart, and positioned so that they faced each other at a 45° angle. Before each trial, the inverted test tube was first presented to the demonstrator, which rapidly removed the stopper and released the seeds into its food dish. After the demonstrator had fed for 10 s, a blind was placed between the two cages to avoid social facilitation effects, and the test tube was presented to the observer for a 1 min trial. If the observer succeeded in removing the stopper within this 1 min period, it received 0.5 g of mixed seeds delivered to its food dish via a section of plastic tubing. The observers' test tubes were always empty to avoid rewarding accidental openings (e.g. with the head or the back of the neck while trying to escape). If the observer did not succeed, another demonstration-trial cycle was performed 1 min later, up to a maximum of five trials per day. We recorded the number of trials required by each individual to learn the task as the measure of social learning ability. If an individual did not learn to open the test tube within the 20 trials, the ceiling value of 21 was recorded.

Determining Sex and Priority of Access to Food

After the neophobia, innovation and social learning tests, the pigeons were placed in 0.9 x 1.4 x 2.3 m aviaries in groups of four. After a 6-7 days habituation period, two trials of the priority of access to food test were performed on the same day, two hours apart. The apparatus consisted of a large cylinder (15 cm in height, 3.5 cm diameter) filled with mixed seeds, with a small opening at the bottom such that only one pigeon could feed at any given moment. The cylinder was placed on the floor, in the centre of the aviary, for two 10 min trials. The amount of time spent feeding by each bird was recorded. Each individual was then ranked (1 to 4) according to how much time it spent feeding compared to its three companions (1 = most feeding time, 4 = least feeding time) (Giraldeau & Lefebvre 1986; Lefebvre & Henderson 1986). Sex of most individuals (n = 36) was determined by a combination of cloacal examination and behavioural observations of displays while grouped in aviaries.

Part II – Experiments in the Field

Subjects

Free-living urban pigeons at twelve sites on the island of Montreal served as subjects for the field experiments. The sites included (1) Parc Notre-Dame-de-Grâce, (2) Parc La Fontaine, (3) Parc Devonshire, (4) Westmount Park, (5) Square Cabot, (6) Place Norman-Bethune, (7) Carré St-Louis, (8) Strathcona Music Building (McGill University Campus), (9) Stewart Biology Building (McGill University Campus), (10) McLennan Library (McGill University Campus), (11) La Cité, and (12) Parc Claude-Jutra. Distance between the sites ranged from 0.4 to 6.4 km, with an average of 2.2 km. Size, amount of vegetation cover and human disturbance levels varied greatly between sites, ranging from large, wooded, quiet parks to small, paved, crowded public squares. Flock size varied from 7 to 175 pigeons depending on the site, but day-to-day fluctuations in numbers for a given site were minimal. Other bird species frequently encountered at the sites were ring-billed gulls (*Larus delawarensis*), house sparrows (*Passer domesticus*), American crows (*Corvus brachyrhynchos*) and European starlings (*Sturnus vulgaris*), but these rarely interfered with testing. Because of the proximity of some sites (e.g. Strathcona Music Building and McLennan Library, 0.4 km apart), it is possible that a small number of individuals visited more than one site (Lefebvre & Giraldeau 1984; Lefebvre 1985).

Experimental Procedure

All experiments took place between May and August 2001. Prior to the beginning of trials, a specific location at each site, visible and accessible to all flock members, was designated as the feeding area. We also selected an observation area, 10-15 m away from the feeding area and most often partially hidden by a tree or a bush. This is where the experimenter was located during all trials. For two days before the tests began, we visited each site at a specific time and offered 50 g of mixed seeds at the feeding area to habituate the pigeons to the time and place of feeding. On test days, we recorded the number of pigeons present at each site. All trials were taped on a video camera, mounted on a tripod at the observation area, and data were obtained later from these tapes. Each flock was submitted to two tests in the same order: neophobia and innovation. We did not conduct a social learning test in the field because it would have been impossible to exclude individual learning through the same controls as those used in captivity.

Neophobia Test

The neophobia test featured two novel object and two control trials over two consecutive days. The type of trial (novel object or control) given first was randomly determined each day; the second trial that day featured the opposite condition, and was presented after a 5 min pause. During the novel object trials, 50 g of mixed seeds was offered at the feeding area on a 10 x 15 cm piece of wire mesh to facilitate retrieval after trials, and an additional 10 g was tossed into the air to attract the pigeons. The experimenter then returned to the observation area, and waited for the first pigeon to begin feeding. If no pigeons showed interest in the food within 20 min, the trial was stopped and another trial was attempted on a subsequent day. Once the first bird had fed for 10 s, the feeding area was approached slowly, the novel object was placed 15 cm away from the food, and another 10 g of seeds was tossed. The experimenter backed away to the observation area and recorded the latency to resume feeding in the presence of the novel object. If no bird returned to the food within 20 min, a ceiling latency of 1201 s was recorded. As in the captive tests, we chose objects unlikely to have been encountered by the flocks in the past, and the order of presentation of the two objects was randomly determined. Control trials were conducted in the same way, but the experimenter touched the ground 15 cm from the food instead of placing a novel object. The mean latency to resume feeding in the control trials was subtracted from the mean latency in the novel object trials to yield the neophobia score.

Innovation Test

We presented the Plexiglas box used in the captive innovation test at each site for a maximum of two trials over two consecutive days. At the beginning of each trial, 10 g of seeds was tossed into the air at the usual feeding area to attract the pigeons. The experimenter returned to the observation area and waited 10 s from the moment the first bird began to feed. The feeding area was then approached slowly, the Plexiglas box, filled with seeds, was placed on the ground, and another 10 g of seeds was tossed. The latency to open one of the lids or drawers was recorded. If success did not occur within 20 min, we conducted another 20 min trial the next day. A ceiling latency of 2402 s was recorded if none of the birds at the site succeeded within the two 20 min trials. Two modes of opening were distinguished: reliable openings, when a bird was clearly seen, either directly or on videocassettes, opening a drawer or lid with the beak; and questionable openings, when a lid was opened accidentally with the foot while a pigeon walked on top of the box, or when pigeons were in such large numbers at the box that it was impossible to see, either directly or on the videocassettes, how the box was opened. To be conservative, the ceiling latency was assigned to all questionable openings.

Data Analyses

We log transformed all data collected during the captive study for normalization purposes ($\log_{10} [x + 1]$) and used parametric statistical procedures. The results of the first neophobia test served to look for the confounding effect of this variable on innovation and social learning; results of the second neophobia test were used only to look for changes over time in fear of novel objects. We used non-parametric statistical procedures to analyse the field data as normalization was not possible.

Results

Part I – Experiments in Captivity

Performances on the innovative problem-solving and social learning tasks were strongly correlated ($r = 0.740$, $p < 0.001$) (figure 3.2 A); individuals that solved the Plexiglas box problem quickly also learned readily from a demonstrator, and vice-versa. More importantly, when social learning and problem-solving were regressed separately against neophobia to remove the effect of this intervening variable, their residuals remained significantly correlated ($r = 0.709$, $p < 0.001$) (figure 3.2 B). Neophobia was positively associated with both social learning ($r = 0.344$, $p = 0.026$) (figure 3.3 A) and problem-solving ($r = 0.312$, $p = 0.044$) (figure 3.3 B).

In the problem-solving test, 35 subjects were successful in opening and feeding from the Plexiglas box. Of the seven that did not succeed, four did contact the box during the 30 min trial. The number of sections of the box contacted varied from 0 to 11, and the number of pecks ranged from 0 to 462. In a multiple regression, latency to contact ($p < 0.001$) and number of pecks ($p = 0.012$) were the best predictors of problem-solving ($R^2_{adj} = 0.777$, $F_{2,39} = 72.493$, $p < 0.001$). Number of sections contacted did not remain in the final regression model because of its association with number of pecks ($r = 0.843$, $p < 0.001$).

No subject solved the social learning task during the 20 min control trial for spontaneous opening, indicating that all successful openings of the tube during the experimental trials were a product of social learning. Of the 42 pigeons tested, only seven failed to learn the task after watching 20 demonstrations, and of those seven, four were not successful in the problem-solving task either.

In the first neophobia test, mean latency to resume feeding after interruption by the experimenter was significantly higher in novel object trials than in control trials (*t* test: $t = -11.645$, $p < 0.001$), indicating that novel objects elicited fear beyond that caused by the interruption. Scores on the first and second neophobia tests (before and after the innovation test) showed that fear of novel objects decreased over time, with the second test yielding much lower latencies than the first one (*t* test: $t = -8.610$, $p < 0.001$).

Consistently with previous studies on pigeons (e.g. Giraldeau & Lefebvre 1987), sex did not affect performance of individuals on the neophobia (ANOVA: $F_{1,34} = 2.352$, $p = 0.134$), innovation (ANOVA: $F_{1,34} = 2.696$, $p = 0.110$) or social learning tests (ANOVA: $F_{1,34} = 0.464$, $p = 0.501$), and there were no significant differences in performance on the three tests in birds with different ranks on the priority of access to food test (ANOVA: neophobia: $F_{1,34} = 1.693$, $p = 0.186$; innovation: $F_{1,34} = 1.226$, $p = 0.314$; social learning: $F_{1,34} = 0.962$, $p = 0.421$).

Part II – Experiments in the Field

In the field, six flocks showed reliable openings and two showed questionable openings of the Plexiglas box within the 40 min time limit, confirming the ecological relevance of the problem-solving task used in captivity. Of the four flocks that did not open the box, two made contact with it. The number of birds present during trials was negatively correlated with problem-solving latency (Spearman rho = -0.560, $p = 0.051$) (figure 3.4; note that figures 3.4 and 3.5 plot the actual data, and not the ranks used in the analyses), indicating that large flocks tended to open the box more rapidly than smaller ones. As in the captive tests, problem-solving was correlated with latency to contact the box (rho = 0.549, $p = 0.064$) and neophobia (rho = 0.505, $p = 0.135$) (figure 3.5), but these associations did not reach the traditional 0.05 significance level. In the neophobia test, mean latency to resume feeding in the novel object trials was significantly greater than in the control trials, demonstrating that the objects caused apprehension in the flocks (Wilcoxon paired-sample test: $p = 0.005$).

Discussion

Three main conclusions can be drawn from this study. First, our results clearly show that innovation and social learning covary between individual feral pigeons (figure 3.2 A); subjects that opened the Plexiglas box quickly were also the more successful ones when learning from a demonstrator. Secondly, the positive association between innovation and social learning was not due to the confounding effect of neophobia. Performances on both the innovative problem-solving task and the social learning task were positively associated with fear of novel stimuli in captivity, and the field study confirmed the association between innovative problem-solving and neophobia. However, when the effect of neophobia on each variable was removed, innovative problem-solving and social learning remained significantly correlated (figure 3.2 B). Finally, the innovative problem-solving test in the field validated the ecological relevance of the captive task; free-living pigeons were also able to open the Plexiglas box. Success in captivity could therefore not be attributed solely to features of the testing situation such as food deprivation, lack of alternative feeding options and forced proximity to the apparatus. The Plexiglas box problem was solved by eight of 12 flocks in the field test (six reliable and two questionable openings), and 35 of 42 subjects in the captive test.

A number of studies have demonstrated positive associations between cognitive traits. Our findings that innovation and social learning covary and that neophobia is positively associated with both cognitive traits in feral pigeons are consistent with this general pattern. Timmermans et al. (2000) have shown that innovation and individual learning are strongly correlated in the two largest comparative studies available on birds (Gossette 1968: 8 species; Sasvári 1985b: 7 species). Lefebvre and Giraldeau (1996), in a re-analysis of Sasvári's (1979; 1985a; 1985b) data, revealed a positive correlation between individual and social forms of learning in five species of Passeriformes. Lefebvre et al. (2002) found that tool-use reports have a similar taxonomic distribution to that of innovation reports in the avian literature. Finally, neophobia was shown to be associated with interspecific differences in innovative problem-solving (Webster & Lefebvre 2001), social learning (Whittle 1996), and individual learning (Seferta et al. 2001) in birds. Reader and Laland (2002) have obtained similar results in primates; they found that innovation, social learning and tool-use are all positively correlated across species.

Lefebvre and Bolhuis (2002) proposed that correlations between cognitive traits may be an interesting tool for investigating the idea that animal brains are modular. Modules have been defined as domain-specific computational mechanisms that are informationally encapsulated and autonomous (Fodor 1983; 2000). In Fodor's view, input systems are modular, but problem-solving abilities are controlled by general purpose processes. Negative correlations, across individuals or species, between cognitive traits, would suggest a trade-off in memory or brain space. Zero correlations could indicate that the traits are independent. Positive correlations would suggest that the traits are part of the same system and that they have been selected together. The large number of intra- and interspecific positive correlations found between innovation, social learning, individual learning, neophobia and tool-use clearly fall in the third category.

Previous studies on innovation (Webster & Lefebvre 2001) and social learning (Whittle 1996) indicate that fear of novel stimuli plays an important role in the performance of individual birds on cognitive tests. Neophobia could mask the true relationship between innovation and social learning in two different ways. First, if innovation and social learning are both positively associated with fear of novel stimuli (figures 3.3 and 3.5), a positive correlation between them could be spuriously caused by their common association with this third, intervening variable. To control for the potential confounding effect of neophobia, we measured fear of novelty for each subject prior to the cognitive tests. We then statistically removed this effect for each the innovation and social learning variables, and found that the two traits remained strongly correlated (figure 3.2 B). Neophobia may be a key intervening variable in many novel situations, but it was not responsible for the positive correlation between innovation and social learning observed in our pigeons. The second way neophobia could mask the relationship between innovation and social learning is by creating a spurious negative relationship between them. If subjects become increasingly habituated to novel stimuli as they are exposed to more tests, subjects who do poorly on the first test because of neophobia will do better on the second one as their neophobia decreases. If test order is counterbalanced or randomized, this alone will cause a negative correlation between the traits (Beauchamp et al. 1994). To overcome this problem, we tested neophobia before and after the innovation test in captivity. In the captive tests, mean latencies to resume feeding in the presence of novel objects decreased significantly between the first and second neophobia test. This result confirmed that neophobia decreased gradually as the pigeons were exposed to more tests, and justified our decision to present the innovation and social learning tests to all birds in the same order.

The problem-solving task used to assess innovativeness in this study involved the apparatus designed and used by Webster and Lefebvre (2001), but resulted in very different success rates. In our study, 35 pigeons out of 42 (83%) in captivity and eight flocks out of 12 (67%) in the field succeeded in opening and feeding from the Plexiglas box. In contrast, only six out of 75 (11%) individuals from five West Indian species successfully opened the box in Webster and Lefebvre's (2001) captive test. Moreover, when we look at results on the two species that are taxonomically closest to our pigeons, the doves *Zenaida aurita* and *Columbina passerina*, success rate is even lower; only one individual out of 30 (3%) solved the problem in captivity and no dove opened the box in the field. In a study of individual learning and neophobia, Seferta et al. (2001) also noticed a marked difference in performance between feral pigeons and *Zenaida aurita*. When data on reversal learning on 8 avian species (taken from Gossette 1968) is examined, pigeons again are outliers and perform much better than expected from their innovation rate and brain size (Timmermans et al. 2000; Lefebvre & Bolhuis 2002). This apparent superiority of pigeons is probably a result of artificial selection. All pigeons in the New World descend from captive individuals and are thus presumably bred for tolerance of captive conditions and human proximity (Johnston & Janiga 1995). It is not a coincidence that feral pigeons are often the species chosen in captive experiments; they tolerate experimental conditions much better than many other species, and consequently perform well on a variety of tasks. It would be important to conduct a similar study on a species that has not gone through artificial selection to make sure the positive correlation between innovation and social learning found here is a general one.

Of the variables measured during the innovative problem-solving task in captivity, the best predictors of latency to open the Plexiglas box were latency to contact the box and number of pecks to the box. Number of sections contacted did not remain in the final regression model because of its association with number of pecks. In the field, latency to contact the box was also weakly correlated with problem-solving. Therefore, a bird that contacted the box promptly, and made several attempts to open it by pecking at various sections either a few times or repeatedly was more likely to solve the problem rapidly. The number of pigeons present at each site was also associated with innovative problem-solving in the field experiments (figure 3.4). Visalberghi et al. (1998) demonstrated that in novel situations, social facilitation accelerated the familiarization process in capuchin monkeys (*Cebus apella*). A similar process is likely occurring in pigeon flocks; participation in flocks allows individuals to observe and respond to the behaviour of others. Pigeons may use conspecifics to obtain information about the risks associated with novel situations; for example, seeing other birds feeding beside the Plexiglas box may be construed as an indication of safety. Individuals in large flocks may also take advantage of the dilution of predation risk to approach and feed from novel food sources. Another factor may underlie this association between number of pigeons and problem-solving; the field experiments were conducted in city parks and public squares, where the frequency and quantity of provisioning by humans varied. It is very likely that large flocks occurred mostly where provisioning was regular and abundant, and as a result those flocks were less hesitant to feed from the experimental food sources.

In 1983, Wyles et al. recognized the potential evolutionary consequences of social learning and innovation; they suggested that the simultaneous presence of both traits in large-brained species may have an accelerating effect on evolution. Social learning in animals may lead to the transmission of innovative behaviours; if these new behaviours expose their bearer to a wider array of environmental conditions, they can increase the rate at which favourable mutations are fixated by natural selection. Wyles et al. (1983) called this accelerating effect *behavioural drive*. The behavioural drive hypothesis recognizes the importance of the simultaneous presence of innovation and social learning, but makes no predictions on the relationship between the two traits within species. We can imagine, however, that the nature of the relationship would have evolutionary implications as well. A mathematical model is needed to investigate this idea further, but in the meantime we can speculate about the potential consequences of different types of correlations.

Let us imagine a population with a strong positive correlation between innovation and social learning and where there are two types of individuals; type A individuals are good innovators and good social learners, while type B individuals cannot invent nor copy new behaviours. Consequently, type A have access to all behavioural innovations available in the population; they obviously rely on their own innovations, and can learn the innovations of others through social learning. Type B have access to zero innovation. In the opposite case of a strong negative correlation, type C individuals would be good innovators and poor social learners, and type D individuals are poor innovators and good social learners. In this case, type C only have access to their own innovations, while type D can rely only on the innovations of others. In this scenario, all individuals have access to some innovations, as opposed to the previous one where some individuals had access to all innovations and others had access to none. A positive correlation between innovation and social learning is thus likely to cause a greater fitness differential between individuals than does a negative correlation, leading to faster natural selection. Payoffs will obviously depend on the risks associated with innovation, as well as the exact nature of the benefits it provides, which might minimize starvation risks in bottleneck situations rather than increase mean payoffs on a day-to-day basis. The potential errors of public information may also be relevant, where information cascades can cause socially-influenced behaviours to drift away from the environmentally optimal condition. Formal models are an obvious next step to obtain a better understanding of the evolutionary consequences of a positive correlation between innovation and social learning.

FIGURE 3.1 Schematic view of the clear Plexiglas box used in the problem solving task in captivity and in the field. Black dots represent metal rings that could be used to pull or push open drawers and to remove lids. Numbers 1-13 indicate sections of the box used to calculate the "# of sections contacted" variable (modified from Webster & Lefebvre 2001).

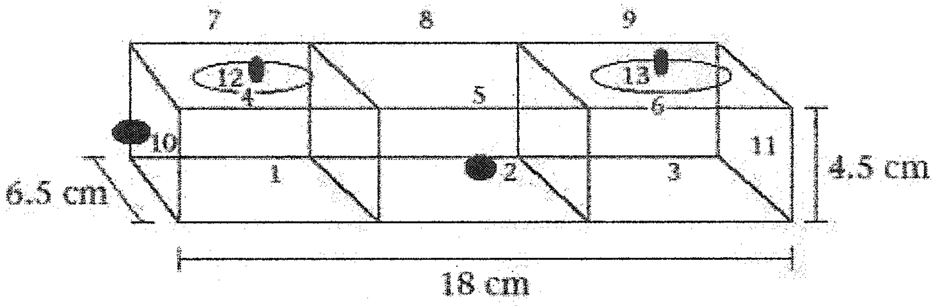

7
8
9
12
13
4
5
6
10
11
1
2
3
6.5 cm
4.5 cm
18 cm

FIGURE 3.2 The relationships between (A) social learning and problem-solving, and (B) residual social learning and residual problem-solving, both regressed against neophobia.

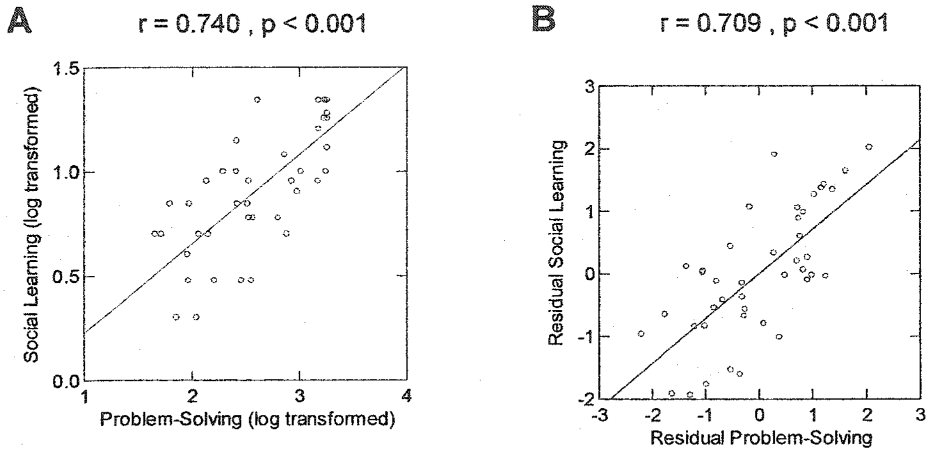
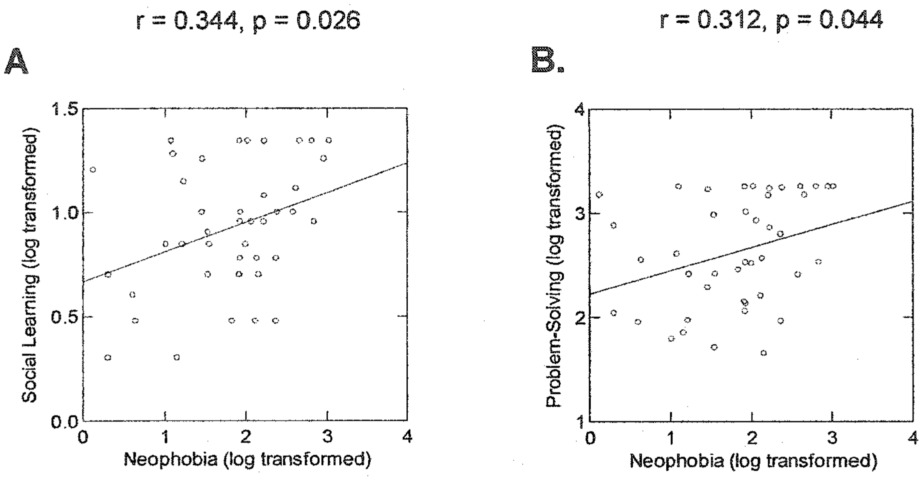

A
r = 0.740 , p < 0.001
Social Learning (log transformed)
1.5
1.0
0.5
0.0
1
2
3
4
Problem-Solving (log transformed)
B
r = 0.709 , p < 0.001
Residual Social Learning
3
2
1
0
-1
-2
-3
-2
-1
0
1
2
3
Residual Problem-Solving

FIGURE 3.3 The relationships between neophobia and (A) social learning, (B) problem-solving in captivity.


r = 0.344, p = 0.026

r = 0.312, p = 0.044

FIGURE 3.4 The relationship between number of birds present at the site and problem-solving latency in the field. The Spearman rho value was calculated from the ranks of the data presented in the figure.

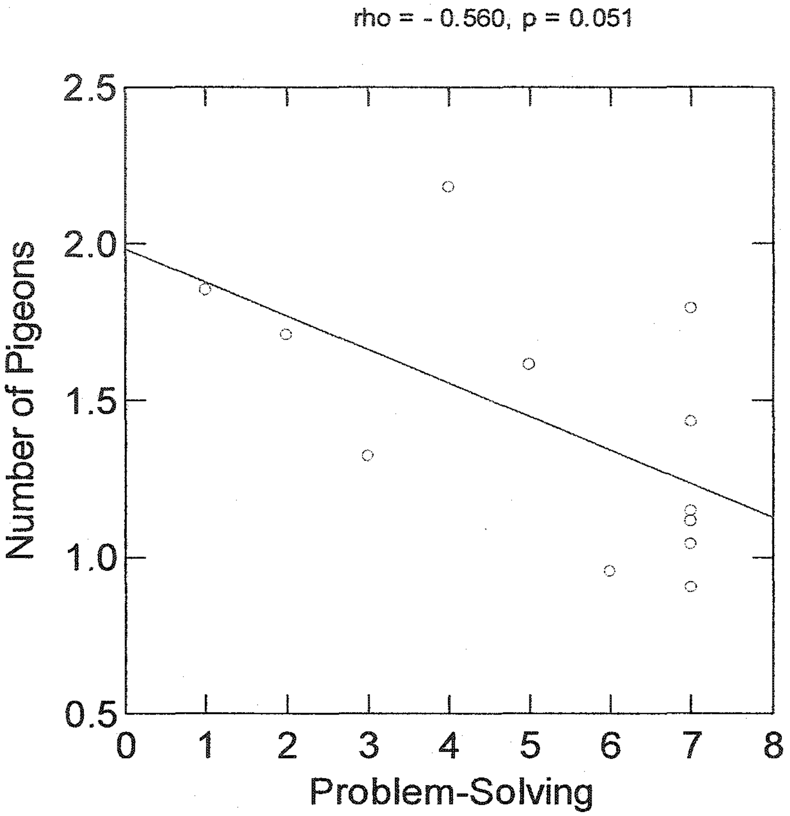
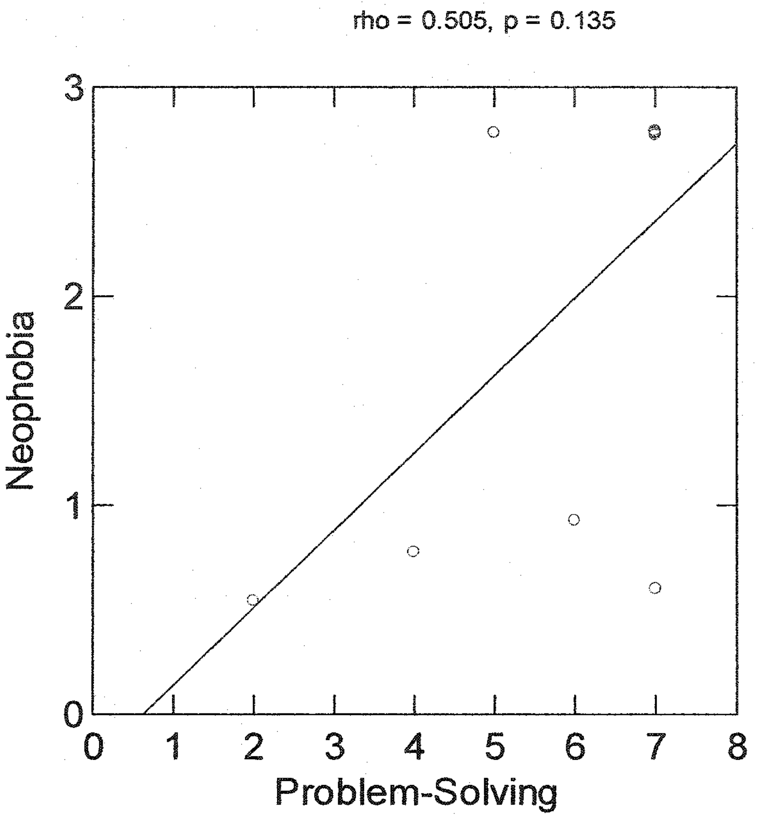

rho = - 0.560, p = 0.051
Number of Pigeons
2.5
2.0
1.5
1.0
0.5
0
1
2
3
4
5
6
7
8
Problem-Solving

FIGURE 3.5 The relationship between neophobia and problem-solving latency in the field. The Spearman rho value was calculated from the ranks of the data presented in the figure.


rho = 0.505, p = 0.135
Neophobia
0
1
2
3
Problem-Solving
0
1
2
3
4
5
6
7
8

GENERAL CONCLUSION

The main focus of this thesis was to determine the relationship between innovation and social learning in birds. Reader and Laland (2002) had previously found these cognitive traits to be positively associated across primate species, and I arrived at the same conclusion in the research on birds presented here. The positive correlation between innovation and social learning was confirmed at several taxonomic levels, and using various types of data. First, I showed that the two traits may be associated at higher taxonomic levels (molecular orders and parvorders) using anecdotal data collected in the avian literature. This interspecific analysis needs to be supported on a larger database, given the small number of reports and their concentration in a single taxon. The tentative interspecific trend was further supported by the correlation between innovation and social learning between species found in a re-analysis of the comparative research of Sasvári (1985a). Finally, laboratory experiments on captive pigeons showed that innovation and social learning are positively correlated between individuals of the same species. That similar results were obtained in three separate analyses in birds and one study in primates seems to indicate that the correlation between innovation and social learning might be a general one. However, the relationship should be tested intraspecifically in primates and in other bird species to confirm the trend.

A positive correlation between innovation and social learning has important implications, especially from an evolutionary point of view. If innovation and social learning usually co-occur as implied by a positive correlation, this situation provides a powerful potential for the diffusion of new behaviours within animal populations. If these new behaviours expose individuals to a wider range of novel selection pressures, this creates an important driving force for evolution. Wyles et al. (1983) recognized this potential accelerating effect on evolution in their behavioural drive hypothesis, and the results obtained in this research support their views. Another implication of the positive correlation between innovation and social learning concerns the organization of animal brains. This research was not intended as a test of modularity per se, but it still provides interesting insight into the way animal brains work. If brains are indeed modular as advocated by a number of researchers, and innovation and social learning are two separate cognitive abilities controlled by different modules of cognition, then a positive correlation between them indicates concurrent evolution of the two modules. In Fodor's (1983; 2000) view of modularity, input systems are modular while problem-solving is controlled by a general purpose cognitive process. A positive correlation between innovation and social learning could also indicate that the two traits are controlled by this general purpose process. Finally, the positive correlation found in this research could also result from animal brains being completely non-modular. This leaves us with many speculations about the organization of animal brains, but no definite answers. Modularity is difficult to test, and only negative correlations between cognitive traits can offer stronger comparative support for the idea that animal brains are modular.

APPENDIX 1. Reports of avian social learning in the foraging context.

Taxonomic group	Species	Learned behaviour	Reference
Accipitrida	Haliaeetus leucocephalus	Locating clumped and unpredictable food sources	Knight & Knight 1983
Accipitrida	Neophron percnopterus**	Throwing stones to break ostrich eggs	Alcock 1970
Accipitrida	Pandion haliaetus**	Flying and catching fish by juveniles	Meinertzhagen 1954
Anseriformes	Anas platyrhynchos	Avoiding food dish associated with visual cue and electrical shock	Klopfer 1957
Anseriformes	Anas platyrhynchos	Shaking reeds to obtain snails	Weidmann 1957
Anseriformes	Anas platyrhynchos**	Eating dry corn meal and washing it down with water	Ramsay & Cushing 1949
Anseriformes	Anas rubripes**	Eating dry corn meal and washing it down with water	Ramsay & Cushing 1949
Anseriformes	Anser anser	Pushing wooden bar to open gliding door and gain access to food	Fritz et al. 2000
Anseriformes	Anser anser**	Biting and chewing stems of butterbur	Fritz et al. 1999
Anseriformes	Cairina moschata	Avoiding food dish associated with visual cue and electrical shock	Klopfer 1957
Charadriida	Larus argentatus**	Dropping shellfish on hard surfaces to shatter them	Beck 1982
Charadriida	Larus glaucescens**	Dropping clams on hard surfaces to crack them	Barash et al. 1975

Taxonomic group	Species	Learned behaviour	Reference
Charadriida	Sterna sandvicensis	Locating clumped and unpredictable food sources	Götmark 1990
Ciconiida	Ajaia ajaja	Locating clumped and unpredictable food sources	Kushlan 1977
Ciconiida	Ardea herodias	Locating clumped and unpredictable food sources	Krebs 1974
Ciconiida	Casmerodius albus	Locating clumped and unpredictable food sources	Caldwell 1981
Ciconiida	Egretta caerulea	Locating clumped and unpredictable food sources	Caldwell 1981
Ciconiida	Egretta garzetta	Locating clumped and unpredictable food sources	Erwin et al. 1985
Ciconiida	Egretta thula	Locating clumped and unpredictable food sources	Kushlan 1977
Ciconiida	Egretta tricolor	Locating clumped and unpredictable food sources	Caldwell 1981
Ciconiida	Eudocimus albus	Locating clumped and unpredictable food sources	Kushlan 1977
Ciconiida	Mycteria americana	Locating clumped and unpredictable food sources	Kushlan 1977
Ciconiida	Plegadis falcinellus	Locating clumped and unpredictable food sources	Kushlan 1977
Columbiformes	Columba livia	Removing stopper from inverted test tube to release seeds	Giraldeau & Lefebvre 1987

Taxonomic group	Species	Learned behaviour	Reference
Columbiformes	Columba livia	Pecking correct key to obtain food	Hogan 1986
Columbiformes	Columba livia	Pulling a chain to obtain food	Hogan 1988
Columbiformes	Columba livia	Piercing paper cover of a box containing seeds	Lefebvre 1986
Columbiformes	Columba livia	Pushing aside cover to access food; piercing paper cover to access food	Palameta 1989
Columbiformes	Columba livia	Operating a treadle to obtain food reward using same technique as demonstrator	Zentall et al. 1996
Columbiformes	Columba palumbus**	Locating clumped and unpredictable food sources	Murton & Isaacson 1962
Columbiformes	Columba palumbus**	Looking at what others are eating and copying feeding actions	Murton 1970
Columbiformes	Streptopelia roseogrisea	Eating novel foods; removing lid or pulling open drawer to access seeds	Hatch & Lefebvre 1997
Columbiformes	Zenaida aurita	Opening a covered food dish to obtain seeds	Carlier & Lefebvre 1997
Columbiformes	Zenaida aurita	Eating previously avoided novel food	Dolman et al. 1996
Columbiformes	Zenaida aurita	Removing stopper from inverted test tube to release seeds	Lefebvre et al. 1996
Corvida	Aphelocoma coerulescens	Digging for peanut bits burried in sand at the center of a plastic ring	Midford et al. 2000

Taxonomic group	Species	Learned behaviour	Reference
Corvida	Aphelocoma ultramarina	Relocating caches made by conspecifics	Bednekoff & Balda 1996a
Corvida	Calocitta formosa	Locating, identifying and exploiting suitable food sources	Langen 1996a
Corvida	Calocitta formosa	Opening a door to gain access to food	Langen 1996b
Corvida	Coracina cinerea**	Changing feeding habits and diet when foraging with other species	Hino 1998
Corvida	Corvus corax	Opening a covered box containing food	Fritz & Kotrschal 1999
Corvida	Corvus frugilegus	Locating clumped and unpredictable food sources	Waite 1981
Corvida	Corvus monedula	Locating food and extracting it from a ball of clay	Roell 1978
Corvida	Corvus monedula	Obtaining food from dispenser using same technique as demonstrator	Wechsler 1988
Corvida	Corvus monedula**	Removing or tearing milk bottle tops to drink milk	Hinde & Fisher 1951
Corvida	Cyanocitta cristata	Manipulating pieces of paper to reach otherwise inaccessible food	Jones & Kamil 1973
Corvida	Cyanocitta cristata	Pecking a disk to obtain food	Schildkraut 1974
Corvida	Dicrurus forficatus**	Changing feeding habits and diet when foraging with other species	Hino 1998

Taxonomic group	Species	Learned behaviour	Reference
Corvida	Gymnorhinus cyanocephalus	Relocating caches made by conspecifics	Bednekoff & Balda 1996b
Corvida	Gymnorhinus cyanocephalus	Distinguishing between good and bad seeds; opening the seeds	Ligon & Martin 1974
Corvida	Gymnorhinus cyanocephalus	Removing a lid to gain access to food	Templeton et al. 1999
Corvida	Nucifraga columbiana	Relocating caches made by conspecifics	Bednekoff & Balda 1996a
Corvida	Nucifraga columbiana	Removing a lid to gain access to food	Templeton et al. 1999
Corvida	Pericrocotus ethologus**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Corvida	Pica pica**	Removing or tearing milk bottle tops to drink milk	Hinde & Fisher 1951
Corvida	Psilorhynus morio**	Identifying and catching appropriate food items	Lawton & Guindon 1981
Corvida	Tersiphone mutata**	Changing feeding habits and diet when foraging with other species	Hino 1998
Passerida	Agelaius phoeniceus	Eating novel foods and increasing food consumption	Mason & Reidinger 1981
Passerida	Agelaius phoeniceus	Avoiding or prefering food associated with a specific visual cue	Mason et al. 1984
Passerida	Carduelis cannabina**	Differences between populations in preferred seed diet	Newton 1967

Taxonomic group	Species	Learned behaviour	Reference
Passerida	Carduelis flammea**	Feeding on peach and apricot blossoms	Stenhouse 1962
Passerida	Carduelis spinus**	Differences between populations in preferred seed diet	Newton 1967
Passerida	Carpodacus mexicanus	Avoiding noxious food	Avery 1996
Passerida	Carpodacus mexicanus**	Feeding on nectar from artificial feeders by hovering	Taylor 1972
Passerida	Cephalopyrus flammiceps**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Certhia himalayana**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Chloris chloris	Avoiding unpalatable food associated with a visual cue	Klopfer 1959
Passerida	Chloris chloris**	Feeding on seeds of a shrub-fruit by cracking the stones	Pettersson 1956
Passerida	Erithacus rubecula**	Removing or tearing milk bottle tops to drink milk	Fisher & Hinde 1949
Passerida	Euphagus cyanocephalus	Locating clumped and unpredictable food sources	Horn 1968
Passerida	Ficedula tricolor**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Fringilla coelebs**	Removing or tearing milk bottle tops to drink milk	Fisher & Hinde 1949

Taxonomic group	Species	Learned behaviour	Reference
Passerida	Fringilla coelebs**	Eating previously avoided novel food	Turner 1961
Passerida	Geospiza conirostris	Manipulating sticks to pry food items out of narrow cracks	Millikan & Bowman 1967
Passerida	Geospiza difficilis septentrionalis**	Puncturing the skin of seabirds and feeding on the blood	Bowman & Billeb 1965
Passerida	Muscicapa ruficauda**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Muscicapa sibirica**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Nectarinia dussumieri**	Locating clumped and unpredictable food sources	Greig-Smith 1978
Passerida	Newtonia brunneicauda**	Changing feeding habits and diet when foraging with other species	Hino 1998
Passerida	Parus ater**	Removing or tearing milk bottle tops to drink milk	Fisher & Hinde 1949
Passerida	Parus atricapillus	Removing cover on food tray to otain mealworm	Alcock 1969b
Passerida	Parus atricapillus	Locating clumped food patches; choosing feeding technique	Krebs 1973
Passerida	Parus atricapillus	Opening and drinking from cream tubs	Sherry & Galef 1984
Passerida	Parus bicolor	Locating food sources	Waite & Grubb 1988

Taxonomic group	Species	Learned behaviour	Reference
Passerida	Parus caeruleus	Lifting piece of linen to obtain hidden food	Sasvári 1979
Passerida	Parus caeruleus**	Removing or tearing milk bottle tops to drink milk	Fisher & Hinde 1949
Passerida	Parus carolinensis	Locating food sources	Waite & Grubb 1988
Passerida	Parus major	Approaching successful foragers, whether conspecific or not	Sasvari & Hegyi 1998
Passerida	Parus major	Lifting piece of linen to obtain hidden food	Sasvári 1979
Passerida	Parus major**	Removing or tearing milk bottle tops to drink milk	Fisher & Hinde 1949
Passerida	Parus major**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Parus melanolophus**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Parus montanus	Feeding on novel foods	Mönkkönen & Koivula 1993
Passerida	Parus monticolus**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Parus palustris	Approaching successful foragers, whether conspecific or not	Sasvari & Hegyi 1998
Passerida	Parus palustris	Lifting piece of linen to obtain hidden food	Sasvári 1979

Taxonomic group	Species	Learned behaviour	Reference
Passerida	Parus palustris**	Removing or tearing milk bottle tops to drink milk	Fisher & Hinde 1949
Passerida	Parus rubidiventris**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Parus rufescens	Locating clumped food patches; choosing feeding technique	Krebs 1973
Passerida	Passer domesticus	Locating clumped and unpredictable food sources	Barnard & Sibly 1981
Passerida	Passer domesticus	Avoiding noxious food associated with a visual cue	Fryday & Greig-Smith 1994
Passerida	Passer domesticus**	Activating opening of sliding doors to enter a café and scavenge crumbs	Breitwisch & Breitwisch 1991
Passerida	Passer domesticus**	Removing or tearing milk bottle tops to drink milk	Fisher & Hinde 1949
Passerida	Passer domesticus**	Eating previously avoided novel food	Turner 1961
Passerida	Passer rutilans**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Phyllastrephus madagascariensis**	Changing feeding habits and diet when foraging with other species	Hino 1998
Passerida	Phylloscopus inornatus**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Phylloscopus occipitalis**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977

Taxonomic group	Species	Learned behaviour	Reference
Passerida	Phylloscopus proregulus**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Phylloscopus trochiloides**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Pinaroloxias inornata**	Maintaining feeding specializations (diet and foraging techniques)	Werner & Sherry 1987
Passerida	Prunella modularis**	Removing or tearing milk bottle tops to drink milk	Fisher & Hinde 1949
Passerida	Quelea quelea	Locating clumped and unpredictable food sources	De Groot 1980
Passerida	Quiscalus lugubris	Removing stopper from inverted test tube to release seeds	Lefebvre et al. 1997
Passerida	Quiscalus quiscula	Avoiding or prefering food associated with a specific visual cue	Mason et al. 1984
Passerida	Regulus regulus**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Serinus canaria	Flipping cardboard lid to gain access to well containing food	Palameta 1989
Passerida	Sitta carolinensis	Locating food sources	Waite & Grubb 1988
Passerida	Sitta europaea**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Passerida	Sitta leucopsis**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977

Taxonomic group	Species	Learned behaviour	Reference
Passerida	Sporophila corvina**	Locating clumped and unpredictable food sources	Rubenstein et al. 1977
Passerida	Sporophila torqueola**	Locating clumped and unpredictable food sources	Rubenstein et al. 1977
Passerida	Sturnus vulgaris	Avoiding noxious novel food	Rothschild & Ford 1968
Passerida	Sturnus vulgaris	Removing lid associated with visual stimulus to gain access to food	Templeton 1998
Passerida	Sturnus vulgaris**	Removing or tearing milk bottle tops to drink milk	Fisher & Hinde 1949
Passerida	Tiaris olivacea**	Locating clumped and unpredictable food sources	Rubenstein et al. 1977
Passerida	Turdus merula	Pulling string out of a glass cylinder to access seeds	Sasvári 1985
Passerida	Turdus merula**	Removing or tearing milk bottle tops to drink milk	Fisher & Hinde 1949
Passerida	Turdus migratorius**	Feeding on juniper berries and toyon fruits by hovering	Maclean 1970
Passerida	Turdus philomelos	Pulling string out of a glass cylinder to access seeds	Sasvári 1985
Passerida	Turdus philomelos**	Removing or tearing milk bottle tops to drink milk	Fisher & Hinde 1949
Passerida	Zonotrichia albicollis	Removing cover on food tray to otain mealworm	Alcock 1969b

Taxonomic group	Species	Learned behaviour	Reference
Phasianida	Coturnix japonica	Operating a treadle to obtain food reward using same technique as demonstrator	Akins & Zentall 1996
Phasianida	Coturnix japonica	Pecking an illuminated key to obtain food	Sanavio & Savardi 1980
Phasianida	Gallus gallus	Breaking a membrane on a container and consuming blood	Cloutier & Newberry 2001
Phasianida	Gallus gallus	Choosing foraging sites preferred by demonstrators	McQuoid & Galef 1992
Phasianida	Gallus gallus	Pecking correct colored key to gain access to food	Nicol & Pope 1992
Phasianida	Gallus gallus	Pecking at conspecific's bill tip and inadvertantly obtaining food	Tolman & Wilson 1965
Phasianida	Gallus gallus	Eating previously avoided novel food	Turner 1964
Phasianida	Gallus gallus	Running a straightaway with food reward at the end	Smith 1957
Piciformes	Dendrocopos himalayensis**	Locating clumped and unpredictable food sources	MacDonald & Henderson 1977
Piciformes	Dendrocopos major**	Removing or tearing milk bottle tops to drink milk	Hinde & Fisher 1951
Piciformes	Picoides pubescens**	Locating food patches and choosing most efficient feeding technique	Sullivan 1984
Piciformes	Picoides villosus**	Locating food patches and choosing most efficient feeding technique	Sullivan 1984

Taxonomic group	Species	Learned behaviour	Reference
Psittaciformes	Eolophus roseicapilla**	Choosing and obtaining food	Rowley & Chapman 1986
Psittaciformes	Forpus conspicillatus	Foraging is synchronised in most group members	Garnetzke-Stollman & Franck 1991
Psittaciformes	Melopsittacus undulatus	Opening a covered food dish to obtain seeds	Dawson & Foss 1965
Trochiliformes	Archilochus colubris	Feeding from a novel nectar source (a syringe)	Altshuler & Nunn 2001
Trochiliformes	Selasphorus platycercus	Feeding from a novel nectar source (a syringe)	Altshuler & Nunn 2001
Tyranni	Megarhynchus pitangua**	Avoiding noxious food	Cook et al. 1969
Tyranni	Myiodynastes maculatus**	Avoiding noxious food	Cook et al. 1969
Tyranni	Tyrannus savana	Eating previously avoided food	Alcock 1969a
Tyranni	Tyrannus savana	Removing cover on food tray to otain mealworm	Alcock 1969b

** denotes field anecdotes

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