INFORMATION TO USERS

This manuscript has been reproduced from the microfilm master. UMI films the text directly from the original or copy submitted. Thus, some thesis and dissertation copies are in typewriter face, while others may be from any type of computer printer.

The quality of this reproduction is dependent upon the quality of the copy submitted. Broken or indistinct print, colored or poor quality illustrations and photographs, print bleedthrough, substandard margins, and improper alignment can adversely affect reproduction.

In the unlikely event that the author did not send UMI a complete manuscript and there are missing pages, these will be noted. Also, if unauthorized copyright material had to be removed, a note will indicate the deletion.

Oversize materials (e.g., maps, drawings, charts) are reproduced by sectioning the original, beginning at the upper left-hand corner and continuing from left to right in equal sections with small overlaps. Each original is also photographed in one exposure and is included in reduced form at the back of the book.

Photographs included in the original manuscript have been reproduced xerographically in this copy. Higher quality 6" x 9" black and white photographic prints are available for any photographs or illustrations appearing in this copy for an additional charge. Contact UMI directly to order.

UMI

A Bell & Howell Information Company
300 North Zeeb Road, Ann Arbor MI 48106-1346 USA
313/761-4700 800/521-0600

THE RELATIONSHIP BETWEEN SCRAMBLE COMPETITION AND SOCIAL LEARNING: A NOVEL APPROACH TO TESTING ADAPTIVE SPECIALIZATION THEORY

by

Patrick J. Whittle

Department of Biology
McGill University

December 1996

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfilment of the requirements for the degree of Master of Science.

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Acquisitions et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence

Our file Notre référence

0-612-29809-4

Canada

ABSTRACT

This thesis examines whether scramble competition is associated with social learning. The question is explored via a comparative study involving two species of grassfinches, Amadina fasciata, and Taenopygia guttata. These finches vary in the degree to which they employ scramble competition while foraging, but are otherwise similar behaviourally and morphologically. General problems associated with the application of the comparative method to the testing of learning specializations are discussed. Functional improvements to previously employed approaches are proposed, and then implemented in a novel methodology and statistical approach to analysing the data, the Manova approach. The results of the study suggest that there is no link between scramble competition and social learning in these two species. When the effects of confounding variables are removed from the interspecific comparison, the species do not appear to differ in their social learning abilities. The results also indirectly suggest that some forms of social learning occur through the mechanisms of general learning.

RÉSUMÉ

Cette thèse examine la relation entre la compétition par la vitesse et l'apprentissage social. La problème est exploré via une étude sur deux espèces de pinsons, Amadina fasciata, et Taenopygia guttata. Quand ils s'alimentent, ces pinsons diffèrent par leur utilisation relative de la compétition par la vitesse et la compétition agressive; ils sont par ailleurs très semblables du point de vue morphologique, taxonomique et comportemental. Les problèmes associés aux épreuves comparées d'apprentissage sont d'abord discutés. Des améliorations à la méthode comparée sont suggérées et appliquées à une nouvelle méthodologie expérimentale, l'approche par analyse de variance multivariée. Les résultats indiquent qu'il n'y a pas d'association entre la compétition par la vitesse et l'apprentissage social chez les deux espèces de pinsons. Quand les effets des variables confondantes sont enlevées dans la comparaison, les espèces ne diffèrent pas dans leur capacité d'apprentissage social. Les résultats suggèrent que l'apprentissage social est contrôlé par les mêmes mécanismes que l'apprentissage indivduel.

ACKNOWLEDGEMENTS

My initial thanks go out to my supervisor Louis Lefebvre. Professionally, he provided me with a thought-provoking project to work on, and much assistance in its development. Personally, he showed great patience and extended much encouragement in helping me to complete it. I would also like to thank the members of my supervisory committee, Don Kramer, and Luc-Alain Giraldeau, for their input.

For their wonderful care of the birds, I owe much thanks to Sarah Timmermans and Tam Nguyen. I also owe a debt of gratitude to Richard Preziosi and Hugh Tyson for their invaluable help with the statistical analysis, to Bob Lemon for loaning me the bird cages, and to Tony Walsh for his assistance with the technical work. Thanks also to those members of my family who helped me in the writing of this thesis.

Finally, thanks and best wishes to all those friends who provided me with moral support in times of need. In particular, I would like to thank Kate Holmes, Heather Cole, George Lozano, Rebecca Tittler, and David Quance.

Financial support was provided by an NSERC operating grant to Louis Lefebvre, and by teaching assistantships within the Biology department.

TABLE OF CONTENTS

Chapter 1

The Ecological Approach to Learning

The Traditional Approach to Learning

The study of animal learning began with an emphasis on uncovering similarities in the learning mechanisms of different animal species. As an emerging discipline, its role was to provide empirical support for the theory of evolution. To this end, its founders (most notably Darwin and Romanes) had a clear agenda: showing that intelligence was an evolved trait initially required demonstrating continuities in the intellectual abilities of different animal species. Such demonstrations would provide empirical support for the idea that the capabilities of more intelligent animals were derivable from relatively primitive ancestral forms.

The documenting of cognitive continuity by Darwin and his colleagues took the form of collecting literally hundreds of anecdotes from pet owners, zoo keepers, and naturalists, these being stories of learning and insight suggestive of human-like mental abilities. Such accounts played an important role in shaping Darwin's views on the structure of animal cognition, as reflected in the following declaration:

> The difference in mind between man and higher animals, great as it is, certainly is one of degree and not of kind. We have seen that the senses and intuitions, the various emotions and faculties, such as love, memory, attention, curiosity, imitation, reason, etc., of which man boasts, may be found in an incipient, or even sometimes in a well-developed condition, in the lower animals (Darwin 1920, p. 128).

Despite the impressive number of anecdotes, however, it was soon realized that any true insight into animal cognition required more rigorous scientific scrutiny. In this vein, as unbiased evidence for continuity in the learning mechanisms between animals and man, Darwin and colleagues' collection of anecdotes was of questionable validity.

More objective methods for comparing the cognitive abilities of animals were developed by E.L. Thorndike in the United States, and I.P. Pavlov in Russia. They brought the study of animal learning into the laboratory, their work establishing it as a major branch of experimental psychology. Nevertheless, and with profound significance to future views on the structure of learning, the Darwinian agenda of blurring any sharp divisions between humans and animals was retained. Thorndike, for example, in a systematic comparison of fishes, chickens, cats, dogs, and monkeys on a series of analogous learning tasks, concluded, despite clear differences in learning rates among his subjects, that there was little distinguishing their performances qualitatively (Thorndike 1911). He was led to suggest that they were all utilizing the same underlying mechanisms of learning. Their taxonomic diversity further spurred him to conclude that his results could be extrapolated to all species, including humans. Following Darwin's lead, he declared the main purpose of experimental studies as lying in establishing continuities in the learning mechanisms between animals and man. Pavlov, meanwhile, independently reached similar conclusions with respect to the learning principles uncovered in his experiments with dogs (Pavlov 1927).

Later researchers of comparative cognition continued to emphasize the similarities between humans and animals, and by extension, among the animals themselves. Following Thorndike's impetus, of prime concern was demonstrating that mental performance in "higher" animals was driven by the same basic processes operative in lower forms (see e.g. Seligman 1970; Roper 1983; Rozin & Schull 1988). Interest became centered around the mechanisms of learning originally elucidated by Thorndike and Pavlov, now termed instrumental and classical conditioning respectively, and collectively referred to as associational learning. These in turn had become viewed as important aspects of all forms of learning in all animals.

Although species differences were acknowledged, they were generally categorized as examples of instinctual behaviour, in turn thought to stem from an innate hard-wired system designed to permit animals to cope with the problems endemic to their particular environments. Learning, meanwhile, was viewed as a qualitatively different phenomenon, thought to serve the functionally distinct purpose of allowing animals to solve newly arising problems by permitting their behaviour to be modified by experience (Johnston 1982).

Eventually, continuing emphasis on associational learning and on demonstrating continuities led to the development of Darwin's initial thrust into a well-articulated perspective on learning known as General Process Theory (GPT) a theory that quickly came to dominate views on the structure of animal cognition (Shettleworth 1993). At the heart of the general process perspective was the belief that all learning could be decomposed into a few basic associative mechanisms common to all organisms and domains (feeding, reproduction etc.; Rozin & Schull 1988). By this view, learning could now be wholly defined by classical and instrumental conditioning, which themselves were thought to be characterized by a limited set of rigid rules of operation (see Roper 1983). A subsidiary assumption, referred to as the principle of equipotentiality, served to reconcile the general process view with evolutionary considerations. It postulated that learned associations could be formed equally easily between any two arbitrarily chosen stimuli or events (Seligman 1970). Learning, in other words, was independent of context, and thus not subject to qualitative change from variation in selection pressures. In essence, GPT (which with little modification continues to underlie the prevalent view on animal cognition) advocated that learning had not undergone any fundamental evolutionary change since its inception (Bitterman 1975; Shettleworth 1993).

An Alternative Perspective

Towards the end of the 1960's, the ability of GPT to account for all forms of learning began to be seriously questioned by numerous learning theorists (e.g. Garcia et al 1966; Bolles 1970; Seligman 1970; Rozin & Kalat 1971; Shettleworth 1972; Hinde 1973). Dissension stemmed mainly from reoccurring experimental examples of what were termed 'constraints on learning'. These were situations where learning failed to occur as predicted despite adherence to the rules thought to govern the formation of associations, a phenomenon first extensively documented by Breland & Breland (1961).

In many instances, these 'constraints' appeared to be of functional significance to the organism. Perhaps most notable in this regard were the results of Garcia and colleagues (Garcia & Koelling 1966, Garcia et al 1966), whose work raised an uproar among traditional learning theorists when first published. The source of discord was a documentation of the ability of rats to associate flavours, but not audio-visual cues, with an induced illness administered several hours later. The selective nature of the association seemed to violate the principle of equipotentiality, and its formation over such a long delay was also difficult to incorporate into the general process framework, which maintained that associations could not be formed between stimuli paired more than a few seconds apart in time (Roper 1983). Rather, these associational anomalies made functional sense as the products of selection for a system specialized to help avoid toxic foods in nature (see Rozin & Kalat 1971).

The inadequacy of GPT to account for this and other apparent examples of adaptively specialized learning abilities (e.g. Bolles 1970) led to calls for a greater degree of integration of learning theory with biological considerations. The adaptive significance of learning was stressed, and by extension, it was suggested that learning could only be properly understood by relating it to the natural environment (e.g. Bolles 1970; Rozin & Kalat 1971; Shettleworth 1972).

Initially put forth was the idea that animal cognition should be viewed as a collection of specialized abilities, each having evolved independently to serve specific functions (Rozin & Kalat 1971). In their words, learning should be regarded "in the same way as other biological characteristics, subject to natural selection, and therefore adapted to handle specific environmental problems" (Rozin & Kalat 1971 p. 459). However, while Rozin & Kalat's work helped generate widespread interest in the idea of adaptive specializations of learning, their contribution seemed to end with the observation that some learning abilities appeared tailored by natural selection to cope with particular biological demands (Domjan & Galef 1983). Because their evidence for the existence of learning specializations was entirely post hoc, it was open to significant criticism from dissenters (e.g. Bitterman 1975).

It was soon realized that empirically demonstrating learning specializations required some means of predicting their existence a priori, as well as some form of control to rule out other possible interpretations of purported specializations. In this regard, Domjan & Galef (1983) were the first to propose the use of the general framework and methods having proven successful in uncovering and illustrating examples of adaptive specializations of other types of biological traits:

> In our view, problems to be faced in the study of the adaptive specialization of associative processes are not significantly different from those to be faced in the demonstration of the adaptive specialization of morphological features or instinctive behaviours...Our proposal is thus simply for the introduction of modern comparative methods into the study of animal learning" (Domjan & Galef 1983 p. 157).

In keeping with other programmes in evolutionary biology then (see Harvey & Pagel 1991), their suggested approach entailed using ecological variables to forecast the occurrence of adaptive specializations of learning, and methodologically, the use of comparative studies to demonstrate predicted specializations empirically.

Domjan & Galef's work has since spawned a number of derivative approaches, the "synthetic" (Kamil 1988), "adaptive-evolutionary" (Rozin & Schull 1988), and "ecological" (Shettleworth 1993) approaches to animal cognition. In contrast to the general process perspective of a universal, unidimensional selective advantage being afforded by the ability to learn (e.g. Mayr 1974), these approaches (hereafter jointly referred to as the ecological approach) all embrace the view that learning is subject to both qualitative and quantitative change from ecologically imposed variation in selection pressures. In particular, in keeping with the fine-tuned evolution exhibited by other biological traits (e.g. Harvey & Clutton-Brock 1983), specific selective demands on learning are expected to result in the evolution of learning specializations. The latter, as the most compelling evidence for the adaptability of learning to environmental variability, serve as the focus of research for the ecological programme (Johnston 1982; Kamil 1987; Rozin & Schull 1988; Shettleworth 1993).

Evidence for Learning Specializations

Spatial memory in food-storing birds

The primary empirical support for the ecological programme comes from the study of spatial memory in food-storing birds. Species in 12 of the 170 families of birds are known to cache food (Sherry 1985). Research on food-storing behaviour has focused on two of these, the tits (Paridae) and corvids (Corvidae). Within these families, the storing feats of some caching species are quite remarkable. For example, Siberian tits (Parus cinctus) have been estimated to store up to 500 000 items per year. Meanwhile, the most prolific storer among corvids, Clark's nutcracker (Nucifraga columbiana), may cache up to 330 00 pine seeds a year (Vander Wall & Balda 1977). In this species, caching behaviour is known to be accompanied by morphological specializations; a bill shaped to allow the prying of seeds from pine cones, strong flight muscles for the repeated transporting of seeds to cache locations, and finally, a specialized sublingual pouch for carrying large numbers of seeds in flight.

Within the corvid and parid families, there is considerable interspecific variation in the tendency to store food (Shettleworth 1990). Because food storing entails a surplus investment of time and energy, its evolution is contingent on storers being more likely to recover cached food than non-storing competitors (Andersson & Krebs 1978). Since evidence from both the field and the laboratory strongly suggests that this recovery is mediated by spatial memory (reviewed in Shettleworth 1990), the former statement implies a more highly developed spatial memory in food storers than the non-storing members of their families.

Two different sets of comparative studies both indicate that food-storing birds' spatial memory may be adaptively specialized. First, a number of comparative tests have indeed suggested that the memory abilities food storing birds use to retrieve cached food are enhanced relative to closely related non-storers (reviewed in Krebs 1990). Furthermore, interspecific variation in food-storing behaviour has been shown to be correlated with variation in hippocampal volume, a region of the brain known to be associated with spatial memory (Sherry et al 1989; Krebs et al 1990).

Birdsong learning

A second body of evidence relevant to the ecological programme has emerged from the study of song learning in passerines. In all songbirds studied, there appear to be distinct characteristics of learning associated with the process of song development (Sherry & Schacter 1987). To begin with, the acquisition of song appears to be restricted to a particular sensitive period, usually early in the life of most species (Marler 1987). During this sensitive period, learning can generally occur with remarkably few exposures to song (Marler 1990). Nightingales (Luscinia megarhynochos), for example, can learn a conspecific's song accurately following as few as five presentations (Todt et al 1979). In many species, song learned during the sensitive period also appears to be encoded in memory in a distinctly robust fashion. Swamp sparrows (Melospiza georgiana), for example, are known to undergo a silent retention period of several months after song is initially learned (where song is neither heard nor rehearsed) before first producing it (Marler & Peters 1981). Finally, although many songbirds are known to generally be able to learn a great variety of other birdsongs, during the sensitive phase of most species there appear to be innate selective mechanisms to help restrict the songs learned to those of conspecifics (Marler 1990). In this respect, for example, young male song sparrows show a strong preference to learn the songs of their own species even when reared by heterospecifics (Marler 1990).

The unusual characteristics of song learning can be related to the functional significance of song and to the conditions under which birds must learn them. Because songs are used by males to defend their breeding territories and to attract mates, a given song must serve to identify the species of the singer (Sherry & Schacter 1987). It is therefore important that song learning in young birds be restricted to those of conspecifics, that it be accurately learned with relatively few exposures, and that it subsequently be correctly reproduced from memory following a lengthy time gap during which the young bird will not have further opportunity to hear it (Sherry & Schacter 1987).

Problems in Demonstrating Learning Specializations

Despite some compelling examples of possible learning specializations, adaptive specialization theory has not had the influence on conceptions of animal learning that many anticipated at its inception. Although the core ideas of the ecological approach are widely accepted in other areas of evolutionary biology, most learning theorists continue to emphasize general, rather than specialized cognitive abilities (Domjan & Galef 1983; Shettleworth 1993).

This limited impact stems in part from the methodological difficulties associated with illustrating learning specializations. As with adaptive specializations of any kind, empirical demonstrations of learning specializations require the use of comparative tests (Shettleworth 1993). Adaptive specializations of learning are inferred when closely related species are shown to differ on some learning ability, this difference having been predicted a priori on the basis of an interspecific distinction in ecology. A general problem with the comparative method is that of confounds, the possibility that an interspecific difference suggestive of an adaptive specialization is instead attributable to some other extraneous variable. Historically, confounds have been particularly troublesome for comparative learning studies. Inadequacies in traditionally used control measures have allowed critics of the ecological approach to justify rejecting much of the evidence in support of the adaptive specializations perspective (e.g. MacPhail 1982).

There are two general sources of confounding variables associated with demonstrating learning specializations. Because learning ability cannot be directly measured, but must instead be inferred from overt performance, the first of these concerns whether interspecific performance differences suggestive of adaptive specializations are instead the result of disparities in such "contextual variables" (MacPhail 1982) as sensory capacities, motor skills, or motivational levels, rather than a difference in cognition. In brief, the contextual variable problem stems from the impossibility inherent in directly equating experimental conditions (and their accompanying effects on performance) for different animals.

An additional, more subtle source of methodological difficulty lies in distinguishing between interspecific performance differences reflective of adaptive specializations in particular, and those resulting from more generalized differences in learning ability. In this respect, there is considerable evidence that learning may be subject to a generalized scaling effect from a variety of ecological factors; possibilities include differences in brain size or in the size of its components (Rensch 1956; Riddell & Corl 1977; Wyles et al 1981; Lefebvre et al in press), social structure (Dukas & Real 1991; Lefebvre et al 1996), or degree of opportunism (Johnston 1982; Sasvari 1985a,b). The latter, in fact, is one of the basic predictions of contemporary adaptive specialization theory (Lefebvre 1996).

In order to conclusively demonstrate an adaptive specialization of learning, it is critical to control for both above sources of confound. As stated earlier however, previously suggested controls, while of some benefit, have not completely eliminated the problem.

The traditional approach, systematic variation, consists procedurally of repeatedly comparing species on the learning ability hypothesized to be adaptively specialized, while methodically varying levels of particular suspected confounds (Bitterman 1975). A consistent interspecific pattern of performance across tests would imply that the confound under investigation does not differentially influence the compared species. For example, the relative effects of food deprivation on different species can be assessed by comparing interspecific performance across a range of hunger levels. If, for example, one animal were to consistently outperform the other(s), then the relative effects of food deprivation could be rejected as a causal factor in the disparity.

Typically, however, systematic variation alters relative performances enough to suggest a contextual effect, but does not eliminate interspecific differences entirely (Bitterman 1975; MacPhail 1982), thus doing little to alleviate the original problem of ambiguity in attributing cause to the latter. A second major drawback is its inability to control for generalized differences in learning ability, which clearly are not subject to manipulation by the experimenter.

As an alternative to systematic variation, Kamil (1988) has suggested varying the tests of learning themselves. Animals are exposed to several different experiments, each designed to measure the same learning ability, but varying in their procedural details so as to give them different sets of contextual variables. Evidence for an ecological hypothesis would then consist of the species purported to be specialized outperforming the other species on all tests. Similar to the logic of systematic variation then, Kamil's approach seeks to eliminate confounding variables by in effect showing that varying them qualitatively does not alter relative performance. What limits Kamil's approach is its inability to control for any confound with a common effect across tests. Again, this list includes any generalized differences in learning ability between species, as well as such potentially important contextual variables as relative motivational levels or relative levels of neophobia (fear of novelty).

A third, more recent approach (Hilton & Krebs 1990; Shettleworth 1993) seeks to control for all forms of confounding variables by additionally comparing species on learning abilities unrelated to the adaptive hypothesis. An adaptive specialization of learning is inferred when this "baseline" comparison contrasts qualitatively with its adaptive counterpart (in the appropriate direction). In other words, for a significant indication of an adaptive specialization, the species hypothesized to be specialized must, in addition to outperforming the control species on the adaptive test, also perform no better on the baseline test(s).

Use of control tests in this manner can indirectly eliminate both sources of confounding variables. The approach infers the effects of confounds on the adaptive test by extrapolating from relative performance on the control test(s). Thus, if the above conditions are met, the implication is that confounds could not be responsible for the observed disparity on the adaptive test because the results on the control test(s) show that they don't influence relative performance in the appropriate direction. Although a vast improvement on previous suggestions, the approach of Hilton & Krebs (1990) and Shettleworth (1993) is weakened by an overly conservative methodology. Because it relies on qualitative differences between baseline and adaptive performance relationships, its inferential ability is limited to situations where the species hypothesized to have a learning specialization performs less well or equal to the control species on the baseline tests. As such, the approach is unable to discern adaptive specializations in species whose general learning/performance abilities also (independently) exceed those of the control animals (Lefebvre 1996).

A modern comparative approach

While stemming from different sources, confounding variables are endemic to all comparative tests (Krebs 1990). The modern comparative approach for testing adaptive specializations focuses on quantitative, rather than qualitative departures from the interspecific relationship characterizing the relative effects of confounds on the trait in question (Harvey & Pagel 1991). The idea is well illustrated as applied to the familiar confound of body size, with which many biological traits are known to covary allometrically within taxonomic groups (see e.g. Peters 1983). In reference to specific traits, such variation is generally not thought to be related to distinctions in function (Harvey & Pagel 1991). Therefore, in determining if an absolute interspecific difference in the magnitude of some such size-constrained trait reflects an adaptive specialization in one of the species, one compares the magnitudes of the trait after first "subtracting" the corresponding allometric line defining the relative effects of body size from the comparison (Harvey & Pagel 1991). Statistically speaking, this traditionally entails focusing on regression residuals, examining whether relative performance on the adaptive test falls outside the confidence limits of the allometric relationship.

A well known example making use of this idea is the aforementioned comparison of hippocampal sizes between food-storing birds and non-storers. Hippocampal volume is known to be correlated with both brain and body size (Sherry et al 1989; Krebs et al 1990). However, because such variation is not related to interspecific differences in food-storing behaviour, adaptive comparisons of hippocampal volume are made after having statistically removed the effects of these two traits. A second example concerns the comparison of testes size among monogamous and polygynous species of primates (where the adaptive hypothesis is that, due to heightened sperm competition among males, polygynous species should have larger testes; Harcourt et al 1981) Again, testes size varies conservatively with body size, and so, in this comparison the effects of the latter are first quantitatively factored out.

As a more rigorous methodology for the ecological programme, Lefebvre & Giraldeau (1996) have suggested that these same standards be applied to the comparative testing of adaptive specializations of learning (what they term "the residual approach"). Conceptually, the residual approach is similar to that of Hilton & Krebs (1990) and Shettleworth (1993). Species are compared both on control tests designed to measure general performance in the laboratory and on tests designed to measure the learning ability hypothesized to be adaptively specialized. Adaptive specializations are inferred when the same general conditions are met: distinctions in the appropriate direction between relative performance levels on the control and adaptive tests.

However, quantitatively defining interspecific performance on both control and adaptive tests offers the significant advantage of allowing for direct statistical removal of the effects of confounds from the adaptive comparison (statistical approaches for removing confounding variables from tests of learning are reviewed in Lefebvre and Giraldeau 1996). As a result, not only are adaptive specializations more exactly delimited than under the approach of Hilton & Krebs (1990) and Shettleworth (1993), but use of the residual approach also eliminates the dependence on a particular baseline relationship (Lefebvre 1996). Adaptive specializations are simply indicated by significant quantitative differences in performance (in the appropriate direction) on the adaptive test after having factored out the baseline relationship from the comparison.

Not only would adoption of the residual approach render the ecological programme methodologically consistent with other comparative programmes, it would also conform to current theoretical perspectives on the structure of learning specializations. While at its inception, adaptive specialization theory implied that learning consisted strictly of independently evolved, qualitatively distinct learning abilities (Shettleworth 1993), more modern views suggest that many, if not most, adaptive specializations of learning may be structured as quantitative departures from pre-existing, commonly held abilities (Domjan & Galef 1983; Roper 1983; Sherry & Schacter 1987; Rozin & Schull 1988; Shettleworth 1993). In this respect for example, much of the original constraints on learning evidence that initially spawned adaptive specialization theory has been incorporated into the general process framework as quantitative variation in general process mechanisms (see e.g. Domjan & Galef 1983; Roper 1983). The heightened spatial memory of food-storing birds is also thought to be a quantitative augmentation of an interspecifically common system of memory (see Shettleworth 1990). As mentioned above, a qualitative approach to testing for adaptive specializations of learning is much more likely to overlook such quantitatively structured cognitive distinctions, because it cannot detect them unless the species hypothesized to be adaptively specialized also arbitrarily happens to perform no better than the control animal on the baseline tests.

As a final note, it should be mentioned that the residual approach is not inconsistent with the testing of qualitative specializations of cognition. The latter are by definition an all-or-none phenomenon: a species either possesses the ability or it doesn't. Inferences of qualitative specializations are thus more straightforward; on a comparative test indicating such a specialization, the control animal would simply not show the adaptive ability at all, or would use a different, presumably less efficient system of cognition, in which case the specialization would "show" itself empirically in the same way as a quantitative specialization.

Social Learning as an Adaptive Specialization

Social learning, which refers generally to the acquisition of novel environmental information or behavioural patterns through the observation of other animals (see e.g. Whiten & Ham 1992), is often postulated to play an important role in facilitating the development and transmission of adaptive patterns of behaviour among gregarious species (e.g. Emlen & Oring 1977, Galef 1988). Specific suggestions of the adaptive value of social learning are principally derived from teleological considerations. On a broad level, its primary benefit is often proposed to be in providing a more rapid and flexible alternative to genetic transmission in maintaining adaptive behavioural patterns between generations (e.g. Klopfer 1961; Mainardi 1980). Social learning has also frequently been suggested to afford significant individual selective advantages. As put by Galef (1976 p. 78), when contrasted with the relatively error-prone process of individual learning, the "value of the ability of organisms to acquire patterns of behaviour as a result of interaction with conspecifics...is straightforward", more rapid acquisition of behaviours important to fitness. This benefit might apply, for example, to young animals who in the course of their development need to acquire information about the environment pertinent to survival and reproduction (Galef 1976), or to adult organisms living in spatially or temporally patchy environments, where the ability to appropriate conspecific patterns of behaviour might facilitate behavioural adaptation to changing conditions (e.g. Ward & Zahavi 1973).

There is a large body of evidence, primarily derived from field studies, implying that social learning often does provide such selective benefits. There are numerous anecdotal reports of both immature and adult members of many species acquiring information from others, or of behavioural distinctions between different populations of the same species most readily explainable in terms of some sort of socially mediated acquisition of behaviour (examples in Galef 1976; Mainardi 1980; Lefebvre & Palameta 1988; Robert 1990). On a lesser scale, experimental work has indicated that animals may use social learning to appropriate behaviours important to fitness. As illustrative examples, naive rhesus monkeys (Cook et al 1985) and blackbirds (Vieth et al 1980) have shown the ability to learn to recognize potential predators by observing the anti-predatory behaviour of more experienced conspecifics. Similarly, rats (Galef & Wigmore 1983; Strupp & Levitsky 1984) red-wing blackbirds (Mason & Reidinger 1981) and octopus (Fiorito & Scotto 1992) have demonstrated the capacity to acquire foraging cues from others of their species (see Galef 1976; Heyes 1993 for other examples).

However, despite the broad functional benefits of social learning implied by the above theoretical considerations, its taxonomic distribution, while fairly widespread, appears scattered in the literature (Galef 1976; Lefebvre 1996), and on this basis has led some researchers to suggest that social learning may be an independently evolved cognitive specialization (Mainardi 1980; Lefebvre 1996). Mainardi (1980 p. 228), in his review of the social learning literature, stated that social learning occurs "sporadically in the phylogenetic tree", and that consequently "there is little room for doubt that social learning appeared independently various times in the course of evolution". Consistent with this view are instances of fine-grained taxonomic discontinuities in its occurrence. For example, in reviewing the evidence for imitation (a form of social learning) among primates, Whiten & Ham (1992) concluded that apes, but not monkeys, possess the capacity for it. There is also indirect evidence implying that the occurrence of social learning does not correspond taxonomically to more general measures of animal intelligence such as brain size (see above), being implicated in members of relatively small-brained phylogenetic groups such as some species of reptiles and invertebrates, but thought to be altogether lacking in some species of mammals like horses (Baer et al 1983; Baker & Crawford 1986) and cattle (Veissier 1993).

Social learning was in fact the first form of learning for which an ecological framework was proposed. Well before adaptive specialization theory was formally applied to the study of learning, Klopfer (1959, 1961) implicitly did so in linking social learning to both degree of sociality and opportunism. On the basis that social learning is of particular value to gregarious species in "maintaining their respective niches", he stated that "solitary species should be much less likely to have their characteristic behaviour established by observation". He further suggested that conservative species should "show a different type of observational effect" than more opportunistic ones, because opportunistic species by definition encounter more environmental novelty than conservative species, and thus have more to gain from learning the behaviour of others (Klopfer 1961 p. 72-3).

While both of these ecological variables have since been widely cited as presumed correlates of social learning (e.g. Emlen & Oring 1977; Mason & Reidinger 1981; Strupp & Levitsky 1984; Altmann 1989), only three comparative programmes have addressed Klopfer's hypotheses empirically. Klopfer himself (1961) found that, relative to their respective performances in non-social conditions, the great tit (Parus major) was better able to distinguish between palatable and unpalatable food in social (learning in pairs) conditions than the more conservative green finch (Carduelis chloris). Secondly, in a comparison between baboons (Papio ursinus occidentalis), vervets (Cercopithecus aethiops pygerythrus), and mandrills (Mandrillus sphinx), Cambefort and colleagues (Jouventin et al 1976; Cambefort 1981) found that social learning ability was in the same direction as "group cohesiveness" (degree of social structure). Finally, Sasvari's work with passerines (Sasvari 1979; 1985a) suggests that the great tit (Parus major) and blackbird (Turdus merula) are better at social learning than their less opportunistic congeners, the blue and marsh tits (P. caeruleus and P. palustris), and song thrush (T. philomelos), respectively.

Although all of these results are consistent with Klopfer's hypotheses, none of them takes into account possible problems of confound. In linking opportunism with social learning for example, relatively opportunistic species are likely to perform better on any test of learning simply because of a greater tolerance of experimental environments (Lefebvre 1996). Secondly, as previously mentioned, both degree of sociality (Dukas & Real 1991; Carlier and Lefebvre in press a) and opportunism (Johnston 1982) have been postulated as ecological correlates of learning in general. As it turns out, in additional work involving the same species used in their tests of social learning ability, both Klopfer (1961) and Sasvari (1985b) provide interspecific comparisons on non-social measures of learning ability. In reanalysing both sets of social data after first quantitatively removing the non-social performance differences, Lefebvre and Giraldeau (1996) found no significant interspecific distinctions relatable to social learning in particular. Similarly, a comparative study by Lefebvre et al (1996) involving two species of columbids differing in their degree of sociality found consistent interspecific differences on all types of learning tests, whether social or non-social. Carlier and Lefebvre (in press a) further found differences in individual shaping among two populations of Zenaida doves that differ in foraging ecology, social organization and identity of the tutor species they most readily learn from (Dolman et al 1996). These findings suggest that both opportunism and gregariousness select for learning generally.

If there is little direct evidence in support of Klopfer's proposed ecological correlates of social learning, more recent considerations have suggested a link between social learning and mode of foraging competition in group-living animals. Relative to solitary foragers, group foragers face increased competition for food (Lefebvre and Palameta 1988). As a result, individual group members may be expected to exert an additional effort in order to ensure they obtain their share (Clark & Mangel 1986).

Generally speaking, this 'additional effort' may manifest itself behaviourally in one of two ways. Individuals may directly limit a competitor's access to a patch of food by actively defending it, a phenomenon termed interference competition (Miller 1967). Alternatively (such as when food is not economically defendable), group members may compete indirectly with one another by increasing their rates of foraging, a well documented strategy known as scramble competition (examples reviewed in Clark & Mangel 1986; Dolman 1991).

Scramble competition has been implicated both theoretically and empirically as an ecological correlate of social learning. Palameta (1989; Lefebvre & Palameta 1988) has proposed that scramble competition, with its emphasis on speed of foraging, may lead to a "cognitive arms race" between group members, in which selection promotes the evolution of social learning. Under this scenario, an ability to learn others' novel foraging techniques or discoveries of novel sources of food would reduce or eliminate any associated feeding advantage held by the knowledgeable individuals. Indeed, one of the main advantages postulated for group foraging is that being part of a group may increase individual feeding efficiencies by allowing group members to profit from the knowledge of others (Bertram 1978). Any heightened social learning ability might thus function to indirectly increase an individual's foraging rate relative to others in the group.

An additional theoretical link between scramble competition and social learning comes from the work of Giraldeau et al (1994). Under conditions of competitive scramble, access to food is not directly prevented. Therefore, the opportunity for individuals to exploit the food discoveries of others exists, a behaviour known as scrounging (Barnard & Sibly 1981). Giraldeau et al (1994) developed a series of models suggesting that scrounging may interfere with individual learning. Since individual learning is contingent on reinforcement, not only does the time spent by scroungers exploiting the food discoveries of others reduce their own opportunities to learn, but it also reduces others' rates of foraging skill acquisition by reducing the amount of reinforcement they obtain from their discoveries. The models go on to suggest that scrounging behaviour may result in selection for social learning as a means of circumventing the inhibitory effect scrounging has on individual learning. Dolman (1991), in a study focusing on a population of Zenaida doves (Zenaida aurita) in Barbados, was able to demonstrate an empirical link between social learning and scramble competition. Zenaida doves are normally a territorial species that defend their feeding and nesting areas year-round from other doves. While prone to foraging in mixed species aggregations, in such aggregations, interactions between conspecific doves are characterized by relatively high levels of interference competition. Doves attempting to join other doves are almost always met with aggression. In contrast, feeding competition between Zenaida doves and heterospecific members of the aggregation (Carib grackles in particular, Quiscalus lugubris) appears to be predominantly regulated by scramble competition (Dolman 1991).

Dolman (1991) examined the effects of this intraspecific variation in competitive foraging interactions with other species on the ability of doves to learn socially from representatives of either group. The relationship between mode of competition and social learning was quite striking. In a series of experiments, it was found that wild-caught Zenaida doves tended to strongly establish preferences for novel foods based on the feeding behaviours of heterospecific (grackles), rather than conspecific tutors, and also learned a standard social learning task much more readily through observation of a heterospecific tutor than through a conspecific tutor when simultaneously presented with individuals from both species. Because a priori one would expect conspecifics to make better demonstrators (due to the greater overlap in diet and motor skills between tutor and observer), Dolman (1991) suggested that the results she obtained further implicated scramble competition as an ecological correlate of social learning. These conclusions are supported by parallel work on a localized population of group-foraging Zenaida doves that feed off grain spillage in the Deep Water Harbour, Bridgetown, Barbados. These doves, contrary to those that defend territories everywhere else on the island, forage in large homospecific flocks where grackles are rare (Dolman et al 1996). In captive experiments, these group-foraging doves learn from a conspecific tutor, but not from grackle tutors

Thesis Goals

If scramble competition is in fact an ecological correlate of social learning, the possibility also exists, as suggested by Lefebvre & Palameta (1988) and Giraldeau et al (1994), that it may also be an underlying selective pressure. The primary aim of this thesis was thus to determine if the intraspecific relationship between scramble competition and social learning demonstrated by Dolman (1991) was extendable to interspecific cases. Specifically, this study tested the adaptive prediction that interspecific variance in the proclivity to scramble compete is associated with variance in social learning ability. A positive finding in this regard would strongly implicate social learning as an adaptive specialization selected for by scramble competition. A secondary goal of this thesis was to illustrate the a priori application of modern comparative methods to the design and subsequent analysis of a comparative test of learning, and to suggest a novel statistical approach (MANOVA; see methods) in analyzing comparative learning data

Chapter 2

Scramble competition and learning differences between Taeniopygia guttata and Amadina fasciata

The study made use of two morphologically similar species of grassfinches from the family Estrildidae, the zebra finch (Taeniopygia guttata) and the cut-throat finch (Amadina fasciata). The two species are thought to differ in the degree to which they scramble compete with conspecifics while foraging: T. guttata uses scramble competition much more frequently than does A. fasciata, who often aggressively defends food sources against conspecifics (see below, Redman 1995). If the scramble competition hypothesis holds, zebra finches should therefore be better than cut-throat finches in the social learning of foraging information relative to their general learning abilities. The experimental design of this study adopts the general approach advocated by Lefebvre & Giraldeau (1996) as standard procedure in testing for any adaptive specialization of learning. A distillation of the approach, as well as the specifics of its application to this study, are discussed below.

The approach

The residual approach of Lefebvre & Giraldeau (1996) includes five general steps: (1) choose two or more closely related species that differ on an ecological variable hypothesized to select for a learning specialization (Domjan & Galef 1983); to help minimize potential sources of confounding variables a priori, species should otherwise be as similar as possible in phylogeny and lifestyle traits; (2) ensure that the species do not differ on any obvious confounding variables particular to the learning specialization under scrutiny, for example opportunism, anthropophilia or urbanization (lefebvre 1996); (3) test all species using one or more tasks that measure the learning ability predicted to vary in an adaptive way (Kamil 1988); (4) test all species using one or more tasks designed to measure general learning/performance abilities (Shettleworth 1993); (5) test for the adaptive prediction quantitatively, and by comparing relative, not absolute, species differences on the adaptive task (i.e. statistically factor out results of step 4 from the adaptive comparison).

Choice of species

The two species of grassfinches used in this study, A. fasciata and T. guttata, are both considered to be tame, approachable species relatively insensitive to human disturbance. In this regard, both species are commonly kept as cagebirds, and are well known for their ease of maintenance and adaptability to cage life. In the wild, both are gregarious species, usually occurring in large flocks, or occasionally in pairs, but rarely alone. They are of a similar size and have very similar morphologies (apart from coloration). Their natural choice of habitats is virtually identical, both species preferring semi-desert areas of dry brush and scrub. Finally, the two species have matching dietary preferences and feeding behaviours, taking mainly the seeds of grasses, and usually foraging on the ground. The most marked difference between the species suggested in the literature is a greater use of aggression in the cut-throat finch (Goodwin 1982).

To complete the picture presented by the field literature and to validate our use of captive-bred individuals for this thesis, Redman (1995) conducted a preliminary study of foraging interactions in A. fasciata and T. guttata in our laboratory. Redman (1995) placed two mated pairs of the same species in a testing cage containing a small, 5.5 x 5.5 x 5.0 cm feeder with a single (1 cm) hole at the top allowing access to the food (a commercial seed mix for finches). All birds were food-deprived overnight (14 h) prior to testing. Twenty-five trials were conducted for each species; the two pairs used on a given trial were randomly selected from a set of four pairs per species kept in housing cages for the learning experiments of this thesis. Redman (1995) observed the foraging interactions of the four birds that fed on each trial and measured two variables indicative of interference and scramble competition: (i) the average number of individuals simultaneously foraging at the feeder, and (ii) the rate of aggression between group members, defined as the number of pecking or chasing acts per individual per trial. Following Dolman (1991), relative levels of scramble vs.

interference competition for the two species were inferred from interspecific comparisons on the proportion of time spent foraging in groups, as well as levels of aggression among group members.

In the feeding situation used by Redman, aggression rate was an order of magnitude higher in A. fasciata than it was in T. guttata (mean rates 6.7 and 0.4 per bird per trial, respectively; fig. 1a). Redman (1995) also found that zebra finches fed much more often in groups than did cut-throat finches, who were with their mate in the relatively few instances they were not feeding alone (fig. 1b). In contrast, zebra finches fed in groups of 2, 3 or 4 birds more often than they fed alone. When feeding in groups of 2, zebra finches were also less often with their mate than were cut-throat finches. Taken together, the data on aggression and foraging interactions suggest that captive A. fasciata and T. guttata differ sharply in their use of scramble and interference competition at a defendable feeder: A. fasciata are more aggressive and forage more often alone or with their mate, while T. guttata forage unaggressively in groups. Following Dolman (1991), we therefore predict that learning differences between the two species will parallel differences in foraging interactions and that T. guttata will more readily learn from a conspecific tutor than A. fasciata, once the confounding effects of other variables are taken out.

Research design

In the study of learning differences between A. fasciata and T. guttata, eight tasks were presented to the birds in repeated-measures fashion. The tasks themselves could be functionally subdivided into two separate groups, one group (6 tasks) designed to summarize general learning/performance abilities in the laboratory (the control tests), the other group (2 tasks) intended to jointly measure social learning ability (the specifics of the tasks and justification for their use are discussed in later sections). In using a battery of tasks, the aim was to obtain particularly reliable measures of these two behavioural variables. In general, this should be true both for multi-faceted variables (such as general learning/performance abilities) that are difficult to quantify meaningfully on the basis of a single test, as well as more particular variables (such as social learning ability), where repeated measurements help improve the generality of the measure.

Data analysis (i): MANOVA

The primary test of the adaptive hypothesis was done using MANOVA. Generally speaking, MANOVA is ANOVA in which single response (dependent) variables are replaced by families of related ones (Hand & Taylor 1987). Alternatively stated, while in ANOVA dependent variables are directly compared with one another, MANOVA can be used to examine patterns of differences among collections of dependent variables (Wilkinson 1989). Among other situations then, MANOVA is used when "interest lies, not in the raw variables as measured, but in some combination of them" (Hand & Taylor 1987 p. 4). Such was the case in this study, in which the behavioural variables were defined using multiple tasks.

To examine patterns of differences among dependent variables, MANOVA makes use of matrices of numbers referred to as "contrasts". As defined by Hand & Taylor (1987 p. 10), "a contrast on a set of g groups is any set of g numbers which sum to zero". The numbers making up a contrast are applied as weights to the individual groups. As a basic example, the contrast [1 -1] could be applied to two group means to determine whether they differ (equivalent to a t-test; Wilkinson 1989). The value of the contrast would indicate the magnitude of the difference.

Of interest in this study was whether social learning ability differed between the species after having removed the relative effects of general learning/performance from the comparison. To examine this hypothesis, the contrast [1 1 1 1 1 1 -3 -3] was applied to the eight tests of learning/performance. Essentially, this yielded for each individual a multivariate observation comparing a summary measure of the six control tests with a summary measure of the two social learning tasks. The mean intraspecific values of this relative measure of social learning ability were then contrasted between the species, a comparison equivalent to the interaction effect of a species-by-task ANOVA design (see Hand & Taylor 1987 for further details).

While one could thus accomplish the analysis by performing the summations manually a priori, and then contrasting summary values using ANOVA, doing so would result in a substantial decrease in the sample size. Using MANOVA, variance estimates and degrees of freedom remain based on the entire data set (R. Preziosi, pers. comm.).

Data analysis (ii): correlations

The adoption of a repeated-measures design provided a secondary means of evaluating the adaptive hypothesis. It allowed the opportunity to examine how performance on the various measures of learning correlated within a particular species. In assessing possible learning specializations, a negative correlation between an ability hypothesized to be specialized, and more general measures of learning ability, would be consistent with the adaptive hypothesis, under the assumption that different specialized abities are based on mutually exclusive systems (Sherry & Schacter 1987); according to this view, costs incurred for one ability are traded off against a reduction in other abilities. Alternatively, abilities may evolve independently of each other, in which case no correlation is predicted between the tasks assessing them. Finally, a significant positive correlation on the same comparison would imply that a common learning ability was being used in both cases.

In this thesis, there were two ways in which patterns of correlations could provide further support for the adaptive hypothesis. Firstly, if social learning is an independently evolved ability, one indication would be for measures of social learning ability to be more highly correlated (positively) to one another than to measures of general learning ability, within a species. A second source of support would be if the correlations between the zebra finches' individual measures of general and social learning were weaker than the same correlations in the cut-throats, as the adaptive hypothesis predicts that zebra finches' social learning abilities should be more independently evolved.

The control tests

In addition to incorporating two straightforward measures of general learning ability (see below) into the learning/performance summary value, four tasks intended to jointly measure the effects of neophobia/motivation were also included. While the reasons for including a relative measure of motivation in the control tests are self-evident (clearly the speed with which any learning task is solved is partially a function of motivation), the effects of neophobia on tests of learning are less well known. There is, however, evidence suggesting that neophobia is highly significant in this regard. The logic for its inclusion here is thus briefly discussed.

Neophobia, defined as a general aversion to novelty, is well documented in birds and mammals. Evidence also suggests that the intensity of the neophobic response may vary substantially among species (reviewed in Greenberg 1989). Because an animal that actively avoids novel microhabitats will be less likely to exploit such situations opportunistically, Greenberg (1989, 1990) has suggested that the strength of the neophobic response plays an important role in determining the likelihood that an individual will explore, and thus locate, unfamiliar resources. Neophobia may consequently represent an important contextual variable affecting the speed with which learning tests are solved.

By postulating a genetic basis to neophobia, Greenberg (1989, 1990) has further suggested that genetic variation in interspecific propensities for neophobia may underlie relative levels of opportunism across species. Neophobia has been empirically shown to covary with opportunism. In a series of experiments, Greenberg (1983, 1984, 1989, 1990) found that patterns of interspecific differences in levels of neophobia between two species of warbler (Dendroica castanea, D. pensylvanica) and two species of sparrow (Melospiza melodia, M. georgiana) were consistent with external measures of interspecific differences in opportunism. In both cases, the more opportunistic species showed significantly lower levels of neophobia than their respective congeners.

As a control measure, neophobia is thus of relevance to comparative studies of learning for two reasons. In addition to imposing direct contextual effects on the likelihood of an individual solving a learning task, quantitative differences in neophobia among species may underlie interspecific variation in opportunism. If so, degree of neophobia may itself provide an inverse (albeit indirect) measure of general learning ability; as previously discussed, the latter is believed to covary with opportunism (Johnston 1982).

Methods

Subjects

Two replicate groups of 10 pairs (5 of each) of commercially-obtained, adult cut-throat (A. fasciata) and zebra (T. guttata) finches were used as subjects in this study. Birds were housed in male-female pairs on a random basis in individually-labelled wire cages and were kept on a 14:10 hour light:dark cycle. Outside of experimental periods, all birds were provided ad libitum access to commercial mixed finch seed (also used during testing) and water. Birds were housed for a minimum of 7 days prior to any experimentation.

Common elements of procedure

All testing took place in isolation from other birds in a wire cage of dimensions $58 \times 26 \times 33 cm^3$ with a perch located slightly towards one end. The floor of the test cage consisted of a wire grid that allowed seed to fall through, thereby denying birds access to any spilled seed during experiments. Apart from two of the four measures of neophobia (see next section), birds were food-deprived for a period of 14-18 hours prior to experimentation. During testing, the experimenter was positioned to one side of the cage, but was not concealed from the birds. A given bird was subject to a maximum of 10 trials of a given task per day. Order of testing of the birds was randomly determined for each task type, alternating between the species.

Tests of neophobia/motivation

The time required for a given bird to approach and feed from a novel feeder was assumed to jointly vary with both neophobia (directly) and motivation (inversely). Four separate tests of this measure were conducted. The tests themselves varied in terms of two aspects: the type of feeder used (two types), and the amount of food deprivation time involved (two time periods, 7-9 hours and the 14-18 hours used in all other tests).

This arrangement generated four possible combinations (NEO1A, 1B, 2A, 2B; 1=apparatus 1, 2=apparatus 2, A=14-18 hrs., B=7-9 hrs.).

All four tests of neophobia/motivation followed the same basic protocol. A trial consisted of individual birds being presented with one of the two novel feeders for one-minute intervals (figs. 2a, 2b). Feeders were then withdrawn, and following a 30-second withdrawal period, replaced. The feeders themselves were arbitrarily chosen, apart from the requirement of being substantially different from one another and from the variety of feeding dish used in the birds' home cages. Apparatus 1 was a commercially obtained clear plastic feeder (known to have been novel to the birds) of approximate dimensions 10x3x3 cm^3 with a 1.5 cm horizontal protuberance that served to fix the feeder to the cage, as well as dispense the food (fig. 3a). Apparatus 2 was a black cube of dimensions 5.5x5.5x5 cm^3. Food was contained within a small circular depression on the upper surface 1 cm deep and 1.5 cm in diameter (fig. 3b). In both cases the food was clearly visible and accessible to the birds, and feeding thus involved no more than a willingness to approach the feeder. Degree of neophobia/motivation was measured in terms of the number of one-minute trials having elapsed up to and including an initial feeding from the apparatus.

Tests of general learning ability

The final two control tasks were both designed to measure general learning ability. Both of these tasks involved the use of the cube feeder previously used in the neophobia/motivation experiments. Now however, food was concealed with a paper lid fitted with a wire ring (fig. 3b).

The first task (hereafter termed GEN1) involved learning to remove the lid in order to obtain reinforcement. To ensure that the birds regarded the cube feeder as a source of food, and to help them establish that removal of the lid was necessary to obtain reinforcement, individual food-deprived birds were exposed to repeated one-minute presentations of the cube feeder (maximum of 10 per day) within the experimental cage with the depression only partially covered by the paper lid (such that food was still visible and readily accessible), to a point where there was no hesitation in pushing aside the lid for reinforcement in 10 consecutive trials. Also, during experimentation, immediately prior to each set of 10 trials a given bird was given a single presentation of the cube feeder with the lid again only partially covering the depression. Once the bird had pushed aside the lid, it was allowed to feed for 10 seconds.

Actual trials consisted of presenting a loaded cube feeder with the paper lid fully in place (fig. 2b). The lid itself was lightweight, but fit snugly into the depression such that it could no longer simply be nudged aside; instead, revealing the food required pulling on the ring or repeated firm pecking at the lid. Otherwise, the procedure was very similar to that of the neophobia experiments. A trial consisted of a one-minute presentation of the cube. If a bird managed to remove the lid, it was allowed to feed for approximately 5 seconds. The cube was then removed, reloaded if necessary, and replaced following a 30-second interval. The task was considered solved when a bird was able to remove the lid in 8 out of 10 trials. Performance was measured in terms of the number of trials required to reach this criterion level.

The second individual learning experiment (hereafter termed GEN2) required birds to discriminate between two of the cube feeders, identical apart from a rim of masking tape placed around the upper edge of one of them. Both boxes had paper lids covering their depressions; to feed, birds again had to remove a lid. Now however, food was located only in the "taped" cube, which meant that to solve the task the birds not only had to discriminate between the cubes, but also extinguish any tendency acquired during the first experiment to associate the unmarked cube with reinforcement.

Trials consisted of simultaneous presentations of the two cubes, each randomly placed in one of a pair of fixed locations equidistant from the perch (fig. 2c). The only time limit involved was a 5-minute maximum to choose between the cubes, after which time they were removed and randomly replaced (this occurrence was not counted as a trial), but because birds already knew how to remove the lid, the choice between boxes was nearly always made within 10 seconds or less. If a bird removed the correct lid, it was allowed to feed for approximately 5 seconds, after which time the cubes were both removed and randomly replaced following a 30-second time interval (if necessary the taped cube was reloaded during this time). Cubes were immediately removed (and again randomly replaced following a 30-second time interval) if the wrong lid was lifted; birds were not given the opportunity to investigate the taped box. As with the prior learning experiment, a trials-to-criterion of 8 out of 10 correct responses was used to measure relative performance.

Tests of social learning ability

The final two tasks (hereafter termed SOC1 AND SOC2) were both designed to measure each species' ability to acquire foraging cues from a conspecific tutor. Both tasks involved the same basic experimental protocol: naive birds observed tutors obtain reinforcement through a particular manipulation of an apparatus. A wire divider now split the cage in two, physically separating the demonstrators from the naive birds. One of two identical apparati was placed in either side of the cage. Their placement was designed to provide an observer bird sitting on the perch with a similar visual perspective on both items (fig. 2d, 2e).

Trials consisted of exposing naive birds to a single demonstration by a tutor of the procedure to be learned. Following each demonstration, the tutor was allowed to feed from the apparatus for 10 seconds. The tutor's apparatus was then removed for one minute, reloaded and returned to its original position. During this time the observer bird had the opportunity to interact with the version of the apparatus located in its half of the cage. Performance was measured in terms of the number of trials required for an initial performance of the task by the observer bird.

The specifics of the two tasks were as follows: SOC1 involved the pulling of a small block of wood (2x2x2 cm^3) fitted with a wire ring horizontally from a slot (fig. 3c). Pulling out the block caused the tumbling of seeds into the slot from an overhead tube whose opening had been initially covered by the block. A stopper prevented the block from being pushed further into the slot. The "tube feeder" was fixed to a black cube such that the slot was approximately at beak height. The second task, SOC2, involved piercing a foil-covered opaque cylindrical jar (approx. 6 cm in height, 4 cm in diameter) filled with seed (fig. 3d). The foil itself was initially pierced with a ring of tiny holes to aid perforation.

Initially a single, pre-trained tutor was used for the demonstrations. As birds learned to solve the task, three more tutors were eventually added, chosen on the basis of rapidity and consistency of performance. For a given set of demonstrations, a tutor was randomly selected from those available. Following 20 demonstrations (or less if the tutor stopped demonstrating), tutors were substituted.

After experimentation was complete, a third, control group of birds (4 of each species) were individually exposed to each of the two apparati for a maximum of 50 one-minute trials to determine whether there was any spontaneous tendency to solve the task without the benefit of a demonstrator.

Results

Individual scores on each of the various tests of learning/performance are summarized in tables 1 and 2 and diagrammed in fig. 4. Of the 40 birds tested, 34 (18 cut-throat finches, 16 zebra finches) completed all eight tasks. The remaining six birds either died prior to finishing experimentation (4 birds), or served as the initial tutors (2 birds) for the social learning experiments. No members of the control group of birds were able to individually solve either task within the 50 trial limit, justifying the assumption that the measures of social learning were solved through conspecific observation. (In this respect, anecdotal observation suggested that subjects usually watched tutors intently during task demonstration.)

(i) The MANOVA

The results of the MANOVA (summary table in the appendix) are based on the 34 birds who completed all tasks. At face value, they provide no support for the adaptive hypothesis ($F_{(1,32)}= 0.354$, $P=0.556$). In comparing interspecific performance on the two summary measures, the value of contrast indicates that the performance differences between the species on the tests of general and social learning ability are equivalent. Alternatively stated, there is no interaction between the species and the two summary measures of learning ability. There was thus was no absolute interspecific difference on the tests of social learning ability after factoring out general learning/performance abilities from the comparison. This finding is apparent from an informal analysis of the data (fig. 4), as there is little distinguishing the two species on any of the performance measures.

(ii) The correlations

Correlation coefficients between the various measures of learning and neophobia are provided in table 3 for each species; because of the lack of differences revealed by the MANOVA, correlations are also calculated on the pooled data for all birds. Depending on the comparison, sample sizes for pooled data vary from 34 to 40, due to individuals that did not complete the social learning tasks; sample sizes for the data on separate species vary from 15 to 20 for the same reason. Because of the large number of correlations calculated and the consequent probability that several of them will come out significant purely as a result of chance, analysis will focus primarily on the general trends in the table. Overall, tasks show weak positive correlations in the three matrices given in table 3. These trends are illustrated in fig. 5: none of the correlations are negative, but very few reach the 0.05 or 0.01 levels of significance. The mean correlations between tasks for cut-throat finches, zebra finches and the pooled data that includes birds from both species are 0. 261 (SD = 0.144), 0.250 (SD = 0.130) and 0.222 (SD = 0.117) respectively.

Adaptive specialization theory predicts either no correlation (if the abilities are independent) or negative correlations (if the abilities depend on mutually exclusive systems; Sherry & Schacter 1987) between tasks measuring different abilities. In the present case, the data should be interpreted with caution: statistical analysis reveals very few significant correlations, but the general trend suggests a non-random pattern of weak positive ones. Among the correlations for which precise predictions can be made, the two social learning tasks show lower correlations between them (0.292 and 0.098 respectively in A. fasciata and T. guttata) than they do with the general learning tasks (means respectively 0.209, SD = 0.072, for A. fasciata and 0.312, SD = 0.106 for T. guttata); these correlations between general and social learning tasks are higher in zebra finches than they are in cut-throats. Both of these results are contrary those predicted by adaptive specialization, but must be viewed with caution given the low value of the correlations involved.

Discussion

Are the results robust?

The results of this study do not allow a rejection of the null hypothesis; among these two species of grassfinches, an empirically demonstrated difference in the degree to which they scramble compete while foraging does not appear to translate into differing abilities to acquire foraging cues from conspecifics. More generally, there is no suggestion that scramble competition is an underlying selective pressure specific to social learning. The validity of these statements is furthered in that the methods used in this thesis represent substantial improvements over previously used approaches to test adaptive hypotheses: general learning/performance abilities were broadly defined, relative social learning abilities were quantitatively compared, and the species chosen for comparison were otherwise closely matched phylogenetically, behaviourally, and morphologically.

A possible source of concern in the general extrapolation of these results is the assumption made in this thesis that the interspecific distinction in scramble competition observed experimentally by Redman (1995) reflects actual species tendencies in the field. There is the chance that her results may have been biased to elicit this distinction by the experimental conditions she employed. Redman's experimental protocol involved the use of a localized, highly defensible food source. Certainly, based on her results, under these conditions it does appear that cut-throat finches employ scramble competition to a lesser degree than do zebra finches while foraging. However, Grand & Grant (1994) showed that animals may alter the way they compete for food according to the dictates of the environment. In their experiment, in which the spatial predictability of food was manipulated, juvenile convict cichlids (Cichlasoma nigrofasciatum) switched from scramble competition to interference competition as the spatial predictability of food increased (rendering its defence more feasible). By showing that the amount of food eaten correlated positively with mode of competition, Grand & Grant (1994) suggested that the switch occurred because of the changing effectiveness of the two strategies under the differing experimental conditions.

If cut-throat finches are similarly able to alter the way in which they compete for food as warranted by changes in the environment, it may be that actual levels of scramble competition employed by cut-throat and zebra finches in the wild vary less than Redman's results suggest. In the cut-throats' natural habitat, the spatial distribution of food (mainly the seeds of grasses) might render it less economically defensible than it was under the somewhat artificial conditions employed here, resulting in a greater usage of scramble competition by cut-throat finches than was observed by Redman. Furthermore, from the perspective of adaptive specialization theory, learning specializations are assumed to be genetically based; as such, their presence or absence in a particular species should be determined by its natural history. As applied to the hypothesis tested in this thesis then, the relative effects of scramble competition on the two species' social learning abilities depend solely on the degree to which scramble competition is employed by cut-throat and zebra finches in their natural habitats. If actual interspecific levels of scramble competition in the field diverge less than was assumed here, the apparent lack of difference in the social learning abilities of zebra and cut-throat finches may simply reflect this fact, rather than imply rejection of the adaptive hypothesis (although based on field observations, the opportunity for some degree of interference competition does appear to exist in nature; Goodwin 1982).

Converging evidence

This consideration notwithstanding, the findings of this thesis receive strong additional support from further recent work involving Zenaida doves. Tests of social learning ability similar to those employed by Dolman (1991) were conducted on a second population of doves in Barbados (Dolman et al 1996). This population inhabits a harbour area, and feeds primarily on grain spilled in loading areas. These spillages are characterized by being relatively large in size, as well as being spatially and temporally unpredictable (Lefebvre 1996), making active defense uneconomical, and instead promoting the use of scramble competition (Davies & Houston 1984). Indeed, as with the convict cichlids investigated by Grand & Grant (1994), Zenaida doves at grain spillage sites exhibit a change in competitive strategy relative to the territorial flock investigated by Dolman (1991), commonly foraging in large homospecific groups in which conspecifics scramble compete with one another (Dolman et al 1996).

The results of the tests of social learning ability on members of this flock were qualitatively opposed to those of the population investigated by Dolman (1991). Doves from the harbour area were generally able to acquire foraging cues from conspecifics, but did not do so from heterospecific tutors of the species (grackles) preferred by the doves from the territorial population.

While seemingly reinforcing the link between scramble competition and social learning, here the observed difference in social learning ability is intraspecific. Furthermore, because the port population of doves is historically recent, and there is no evidence for it being reproductively isolated, it is unlikely that the two populations studied have diverged genetically (Carlier & Lefebvre in press b). With no genetic distinction between the two populations, the development of different social learning pathways observed in these two groups of doves appears to have been brought about by differing learning schedules, these in turn by-products of the observed qualitative distinctions in their propensities to scramble compete (see below).

Consistent with the results of this thesis then, the second study on Zenaida doves calls into question the presumed selective link between scramble competition and social learning. In the two dove populations, scramble competition does appear to have been related to social learning, but only in generating the necessary conditions for it to occur.

The lack of any observed relationship between scramble competition and social learning in the present study is not incompatible with this interpretation. Here, the presumed differences in potential for interference competition between our two species, suggested by Goodwin (1982) and Redman (1995), appear to have had insignificant effects on the finches' learning abilities. Captive breeding may have masked the potential differences that can appear in the presence of defensible food (Redman 1995). In captivity, breeders try to minimize aggression between birds, both for ethical and commercial reasons related to the risk of injury. Since all the birds used in this thesis were raised in captivity, they probably encountered scramble competition in almost all their foraging interactions. Even if our cut-throat finches were capable of the interference competition revealed by Redman's experiment, they probably had a history of intraspecific scramble competition that was very similar to that of zebra finches. Based on Dolman et al's (1996) data for Zenaida doves and the results of this thesis, extensive experience with intraspecific scramble competition appears to outweigh any pre-programmed difference in the potential use of interference competition. This underlines the point that developmental variables may have been unjustly neglected in the study of ecological correlates of learning. It also suggests that only large differences in natural history, of the type that separate territorial and group-foraging Zenaida doves rather than the mild differences that characterize A. fasciata and T. guttata, appear to lead to robust differences in learning. There may be a parallel to this in the literature on spatial memory, where extreme food storers like Clark's nutcrackers show more robust learning specializations than do Parids (Shettleworth 1993).

Is social learning distinct from general learning?

A broader question to which the results of this thesis pertain concerns whether social learning occurs through the mechanisms underlying associational (general) learning. This possibility was initially raised by the two studies on Zenaida doves. As outlined by Dolman et al (1996), the establishment of tutor preferences in the two dove populations is most parsimoniously explained by referring to basic associational learning paradigms (see e.g. Domjan & Burkhard 1986). Doves from the port area were positively reinforced for attempting to acquire foraging cues from knowledgeable conspecifics, as scramble competition does not prevent one individual from joining another to share in its food find. An equivalent set of contingencies existed between doves from the territorial population and grackles (Dolman 1991). In either case, the end result may have been the formation of a learned association between the response of utilizing either doves (port population) or grackles (territorial population) as sources of foraging information and the obtainment of food. In other words, through the mechanisms of general learning, doves from the port population came to recognize other doves as sources of foraging information, while equivalently, doves from the territorial population came to recognize grackles as such. Both populations then showed the effects of this learning when subsequently presented experimentally with the opportunity to acquire foraging information from either a grackle or a Zenaida dove tutor: territorial doves learned a novel food-finding task from grackle tutors because through previous experience they were biased to do so, while in the same way port doves learned from conspecific tutors.

General learning mechanisms may also be behind the finches' solving of the social learning tasks in this thesis. In this respect, a recent theoretical link between general and social learning of potential relevance to the findings here has been put forth by Heyes (1993 p. 1002):

> Many examples of social learning are equivalent, at a descriptive level, to classical conditioning (general learning). They involve a change in behaviour towards an object or event as a result of exposure to a contingency between that stimulus and some other stimulus. In the case of social learning, conspecific behaviour either brings about stimulus exposure, and/or constitutes the 'other stimulus, but there is no reason to assume that this difference in the conditions of learning, signifies a difference in the process of learning.

In this case, the relevant conspecific behaviour would be the performance by tutors of the responses required to solve the social learning tasks; under Heyes' scenario, the performance of either of these behaviours resulted in naive birds being exposed to a contingency between the corresponding social learning apparatus and food, or alternatively, the tutor finch being reinforced. Through repeated pairings, the apparati themselves may then have come to elicit feeding behaviours from the naive finches in the manner of pigeons directing foraging motor acts towards a light repeatedly paired with food (see Roper 1983). Foraging behaviours normally employed by finches (pecking and pulling of seeds from grasses) directed at the relevant aspects of the social learning apparati (the wire ring or the foil lid) might have been sufficient to solve either problem.

If this extrapolation is somewhat speculative, post-hoc MANOVA comparisons contrasting individual measures of general learning ability with individual measures of social learning ability lend it additional support: there was no interaction effect between species and tasks in any of the four possible contrasts.

[0 0 0 0 1 0 -1 0] $F_{(1,32)} = 0.068$ $p = 0.796$

[0 0 0 0 1 0 0 -1] $F_{(1,32)} = 1.952$ $p = 0.172$

[0 0 0 0 0 1 -1 0] $F_{(1,32)} = 1.360$ $p = 0.252$

[0 0 0 0 0 1 0 -1] $F_{(1,32)} = 0.490$ $p = 0.489$

(each contrast corresponds to a 2x2 ANOVA between species and (non-zero) tasks, with columns 5 and 6 representing the tests of general learning and columns 7 and 8 the tests of social learning)

This indicates that in none of the comparisons between measures of general and social learning did the magnitude of the interspecific performance difference on the general learning test differ statistically from the equivalent measure on the social learning test.

More than simply implying that general learning mechanisms underlay the solving of the social learning tasks, these results suggest that the same learning ability was being used to solve both the general and social learning problems. If the ability used to solve the social learning tasks were distinct (i.e. adaptively specialized) from that used to solve the general learning tasks, one would expect relative interspecific performances on the two test types to be independent from one another.

This finding is not without precedent. As outlined in the introduction, the equivalent trend was seen following the reanalysis by Lefebvre & Giraldeau (1996) of Klopfer's (1959, 1961) and Sasvari's (1979, 1985a, b) data linking opportunism with social learning, and in the interspecific comparison of the social learning abilities of two species of Columbids differing in their degree of sociality (Lefebvre et al 1996). In all cases, differences among the species' general learning abilities were statistically equivalent to differences in their social learning abilities.

In summary, on all known comparative studies measuring social learning for which general learning measures are also available, interspecific differences on measures of social learning appear to be consistent with differences in general learning ability. At the individual level, the data on inter-tasks correlations presented in table 3 and fig. 5 point in the same direction: weak positive correlations characterize all tasks, with trends within a presumed ability (i.e. the two social learning tasks) not being stronger than those that link different abilities. Collectively supporting one another, in all cases the solving of the social learning tasks appears to have occurred via the same ability used to solve the general learning tasks.

Conclusions

(i) Social learning and scramble competition

In conjunction with previous work, the results of this thesis point to two related conclusions. To begin with, there appears to be no relationship between scramble competition and social learning at the interspecific level. In the present study, a clear quantitative distinction in two species' proclivities to scramble compete appears not to have had differential effects on their social learning abilities. After statistically removing general learning/performance abilities from the interspecific comparison, *zebra and cut-throat finches did not differ in their respective abilities to acquire* foraging cues from a conspecific tutor.

In keeping, recent considerations have called into question the original empirical premise behind the social learning-scramble competition selective link. Subsequent work on Zenaida doves by Dolman et al (1996) has suggested that scramble competition was only related to social learning in the territorial population investigated by Dolman (1991) through its inducement of contingencies generating the opportunity for social learning to occur. The lack of a relationship between scramble competition and social learning in the present study is not in contradiction with this view. Here, interspecific variance in scramble competition may have had insignificant effects on the finches' social learning abilities, since the birds rarely encountered the conditions used by Redman (1995) to induce interference competition in cut-throats. .

(ii) Social learning as an adaptive specialization

The second conclusion to which the findings of this thesis pertain is more general. Recent work on Zenaida doves suggests that social learning may occur through the mechanisms underlying general learning abilities, a finding consistent with the work of early investigators of animal learning (reviewed in Galef 1976). The results here, in conjunction with the previous work mentioned above, go beyond this suggestion. They imply that in some cases both general and social learning problems may invoke the same learning ability. In tests involving a total of nine different species (this thesis; Klopfer 1959, 1961; Sasvàri 1985, 1989; Lefebvre et al 1996), despite between-species variance in levels of scramble competition, opportunism, and sociality, interspecific differences on tests of social learning ability remain equivalent to interspecific differences on tests of individual learning ability.

In closing, there are two final considerations worthy of note: to begin with, it is important to mention that social learning is a generic term referring to a number of distinct functional categories (see e.g. Whiten & Ham 1992). More complex forms of social learning (imitation in particular) may be cognitively distinct from simpler forms (Galef 1976; Heyes 1993). Even if the speculations here regarding the relationship between general and social learning are correct, they may only apply to certain forms of social learning.

Secondly, the notion of social learning being governed by general learning mechanisms is not incompatible with it becoming adaptively specialized (e.g. Domjan & Galef 1983; Sherry and Schacter 1987; Shettleworth 1993). As put by Domjan & Galef (1983 p.155):

> The same underlying mechanism may be responsible (with appropriate variations in parameters) for forms of learning that have very different adaptive functions...Thus, adaptive specializations in function are not necessarily the result of specialized mechanisms.

While scramble competition does not appear to be a specific underlying selective pressure of social learning, there may be others that are. To date, too few ecological variables have been tested to entirely dismiss the possibility that social learning may evolve as an adaptive specialization in particular environments.

References

Altmann, S.A. (1989). The monkey and the fig. American Scientist, 77, 256-263.

Andersson, M. & Krebs, J.R. (1978). On the evolution of hoarding behaviour. Animal Behaviour, 26. 707-711.

Baer, K.L., Potter, G.D., Friend, T.H. & Beaver, B.V. (1983). Observation effects on learning in horses. Applied Animal Ethology, 11, 123-129.

Baker, A.E.M. & Crawford, B.H. (1986). Observational learning in horses. Applied Animal Behaviour Science, 15, 7-13.

Barnard, D.J. & Sibly, R.M. (1981). Producers and scroungers: a general model and its application to captive flocks of house sparrows. Animal Behaviour, 29, 543-555.

Bertram, B.C.R. (1978). Living in groups: Predators and prey. In J.R. Krebs & N.B. Davies (Eds.), Behavioural Ecology: An Evolutionary Approach . Oxford: Blackwell, pp. 64-96.

Bitterman, M.E. (1975). The comparative analysis of learning. Science, 188, 160-169.

Bolles, R.C. (1970). Species-specific defence reactions and avoidance learning, Psychological Review, 77, 32-48.

Breland, K. & Breland, M. (1961). The misbehavior of organisms. American Psychologist, 16, 681-684.

Cambefort, J.P. (1981). Comparative study of culturally transmitted patterns of feeding habits in the Chacma baboon (Papio ursinus) and the vervet monkey (Cercopithecus aethiops). Folia Primatologica, 36, 243-263.

Carlier, P. & Lefebvre, L. (in press a). Differences in individual learning between group-foraging and territorial Zenaida doves. Behaviour.

Carlier, P. & Lefebvre, L. (in press b). Ecologically-correlated differences in learning between two adjacent, mixing populations of Zenaida doves. Ethology.

Clark, C.W. & Mangel, M. (1986). The evolutionary advantages of group foraging. Theoretical Population Biology, 30, 45-75.

Cook, M., Mineka, S., Wolkenstein, B. & Laitsch, K. (1985). Observational conditioning of snake fear in unrelated rhesus monkeys. Journal of Abnormal Psychology, 93, 355-372.

Darwin, C. (1920). The Descent of Man and Selection in Relation to Sex (2nd ed.). New York: Appleton

Davies, N.B. & Houston, A.I. (1984). Territory economics. In J.R. Krebs & N.B. Davies (Eds.), Behavioural Ecology: An Evolutionary Approach (2nd ed.). Oxford: Blackwell, pp. 148-169.

Dolman, C. (1991). Preference for a heterospecific demonstrator in a territorial dove. M.Sc. thesis, McGill University, Montréal.

Dolman, C., Templeton, J. & Lefebvre, L. (1996). Mode of foraging competition is related to tutor preference in Zenaida aurita. Journal of Comparative Psychology, 110, 45-54.

Domjan, M. & Galef, B.G., Jr. (1983). Biological constraints on instrumental and classical conditioning: retrospect and prospect. Animal Learning and Behavior, 11, 151-161.

Domjan, M. & Burkhard, B. (1986). The Principles of Learning and Behavior, (2nd ed.). Monterey, California: Brooks/Cole Publishing Company.

Dukas, R. & Real, L.A. (1991). Learning foraging tasks by bees: a comparison between social and non-social species. Animal Behaviour, 42, 269-276.

Emlen, S.T. & Oring, L.W. (1977). Ecology, sexual selection and the evolution of mating systems. Science, 197, 215-223.

Fiorito, G. & Scotto, P. (1992). Observational learning in Octopus vulgaris. Science, 256, 545-547.

Galef, Jr., B.G. (1976). Social transmission of acquired behavior: a discussion of tradition and social learning in vertebrates. Advances in the Study of Behavior, 6, 77-100.

Galef, Jr., B.G. (1988). Imitation in animals: history, definition, and interpretation of data from the psychological laboratory. In T.R. Zentall & B. G. Galef, Jr. (Eds.), Social Learning: Psychological and Biological Perspectives (141-164). Hillsdale: Lawrence Erlbaum.

Galef, Jr., B.G., & Wigmore, S.W. (1983). Transfer of information concerning distant foods: a laboratory investigation of the 'information centre' hypothesis. Animal Behaviour, 31, 748-758.

Garcia, J., & Koelling, R.A. (1966). Relation of cue to consequence in avoidance learning. Psychonomic Science, 4, 123-124.

Garcia, J., Ervin, F.R., & Koelling, R.A. (1966). Learning with prolonged delay of reinforcement. Psychonomic Science, 5, 121-122.

Giraldeau, L.-A., Caraco, T., & Valone, T. J. (1994). Social foraging: individual learning and cultural transmission. Behavioral Ecology, 5, 35-43.

Goodwin, D. (1982). Estrildid Finches of the World. Oxford: Oxford University Press.

Grand , T.C. & Grant, J.W.A. (1994). Spatial predictability of food influences its monopolization and defence by juvenile convict cichlids. Animal Behaviour, 47, 91-100.

Greenberg, R. (1983). The role of neophobia in determining the foraging specialization of some migratory warblers. American Naturalist, 98, 444-453.

Greenberg, R. (1984). Differences in feeding neophobia in the tropical migrant warblers, Dendroica castanea and D. pennsylvanica.. Journal of Comparative Psychology, 98, 131-136.

Greenberg, R. (1989). Neophobia, aversion to open space and ecological plasticity in Song and Swamp sparrows. Canadian Journal of Zoology, 67, 1194-1199.

Greenberg, R. (1990). Feeding neophobia and ecological plasticity: a test of the hypothesis with captive sparrows. Animal Behaviour, 39, 375-379.

Hand, D.J. & Taylor C.C. (1987). Multivariate analysis of Variance and Repeated Measures: a practical approach for behavioural scientists. London: Chapman and Hall.

Harcourt, A. H., Harvey, P.H., Larson, S.G. & Short, R.V. (1981). Testis weight, body weight and breeding systems in primates. Nature, 293, 55-7.

Harvey, P.H. & Clutton-Brock, T. (1983) The survival of the theory. New Scientist, 98, 313-315.

Harvey, P.H. & Pagel, M.D. (1991). The comparative method in evolutionary biology. Oxford: Oxford University Press.

Heyes, C.M. (1993). Imitation, culture and cognition. Animal Behaviour, 46, 999-1010

Hilton, S.C. & Krebs, J.R. (1990). Spatial memory of four species of Parus: performance on an open field analogue of a radial maze. Quarterly Journal of Experimental Psychology, 42B, 345-368.

Hinde, R.A. (1973). Constraints in learning: an introduction to the problem. In R.A. Hinde and J. Stevenson-Hinde (Eds.) Constraints on Learning. London: Academic Press.

Johnston, T.D. (1982). The selective costs and benefits of learning: an evolutionary analysis. Advances in the Study of Behavior, 12, 65-106.

Jouventin, P., Pasteur, G. & Cambefort, J.P. (1976). Observational learning of baboons and avoidance of mimics: exploratory tests. Evolution, 31, 214-218.

Kamil, A.C. (1988). A synthetic approach to the study of animal intelligence. In D.W. Leger (Ed.), Comparative Perspectives in Modern Psychology. Nebraska Symposium on Motivation, (Volume 35, pp. 257-308). Lincoln: University of Nebraska Press.

Klopfer, P.H. (1959). Social interactions in discrimination learning with special reference to feeding behavior in birds. Behaviour, 14, 282-299.

Klopfer, P.H. (1961). Observational learning in birds: The establishment of behavioral modes. Behaviour, 17, 71-80.

Krebs, J.R. (1990). Food-storing birds: adaptive specialization in brain and behaviour. Philosophical Transactions of the Royal Society of London, Series B, 329, 153-160.

Krebs, J.R., Sherry, D.F., Healy, S.D., Perry, V.H., & Vaccarino, A.L. (1990). Hippocampal specialization in food-storing birds. Proceedings of the National Academy of Science (USA), 86, 1388-1392.

Lefebvre, L. (1996). Ecological correlates of social learning: problems and solutions for the comparative method. Behavioural Processes, 35, 163-171.

Lefebvre, L., & Palameta, B. (1988). Mechanisms, ecology, and population diffusion of socially learned, food-finding behavior in feral pigeons. In T.R. Zentall & B. G. Galef, Jr. (Eds.), Social Learning: Psychological and Biological Perspectives (pp. 141-164)). Hillsdale: Lawrence Erlbaum.

Lefebvre, L., & Giraldeau L.-A. (1996). Is social learning an adaptive specialization? In Galef B.G. Jr., Heyes, C.M. (Eds.) Social Learning in Animals: the roots of culture. New York: Academic Press

Lefebvre, L., Palameta, B, & Hatch, K.K. (1996). Is group-living associated with social learning? A comparative test of a gregarious and a territorial species. Behaviour, 133, 241-261.

Lefebvre, L., Whittle, P, Lascaris, E. & Finkelstein, A. (in press). Feeding innovations and forebrain size in birds. Animal Behaviour.

MacPhail, E.M. (1982). Brain and Intelligence in Vertebrates. Oxford: Clarendon Press.

Mainardi, D., (1980). Tradition and the social transmission of behavior in Animals. In: G.W. Barlow and J. Silverberg (Editors), Sociobiology: Beyond Nature. Boulder: Westview/AAAS. 227-255.

Marler, P. (1987). Sensitive periods and the role of specific and general sensory stimulation in birdsong learning. In Imprinting and Cortical Plasticity (ed. J.P. Rauschecker & P. Marler, pp. 99-135. New York: John Wiley.

Marler, P. (1990). Song learning: the interface between behaviour and neuroethology. Philosophical Transactions of the Royal Society of London Series B, 329, 109-114.

Marler, P. & Peters, S. (1981). Sparrows learn adult song and more from memory. Science, 213, 780-782.

Mason, J.R. & Reidinger, R.F. (1981). Effects of social facilitation and observational learning on feeding behavior of the Red-winged Blackbird (Agelaius phoeniceus). Auk, 98, 778-784.

Mayr, E. (1974). Behavior programs and evolutionary strategies. American Scientist, 62, 650-659.

Miller, R.S. (1967). Pattern and process in competition. Advances in Ecological Research, 4, 1-74.

Pavlov, I.P. (1927) Conditioned Reflexes. New York: Oxford University Press.

Peters. R.H. (1983). The ecological implications of body size. Cambridge: Cambridge University Press.

Redman, I. (1995). Different foraging modes of Zebra and Cut-throat finches and their implications on learning studies. Unpublished independent studies report, McGill University.

Rensch, B. (1956). Increase of learning capability with increase of brain size. The American Naturalist, 90, 81-95.

Riddell, W.I., & Corl, K.G. (1977). Comparative investigation of the relationship between cerebral indices and learning abilities. Brain, Behaviour and Evolution, 14, 385-398.

Robert, M. (1990). Observational learning in fish, birds, and mammals: a classified bibliography spanning over 100 years of research. Psychological Record, 40, 289-311.

Roper, T.J. (1983). Learning as a biological phenomenon. In T.R. Halliday & P.J.B. Slater (Eds.), Animal Behaviour (Vol. 3: Genes, Development and Learning, pp. 178-212). Oxford: Blackwell.

Rozin, P. & Kalat, J.W. (1971). Specific hungers and poison avoidance as adaptive specializations in learning. Psychological Review, 78, 459-486.

Rozin, P. & Schull, J. (1988). The adaptive-evolutionary point of view in experimental psychology. In R.C. Atkinson, R.J. Hernnstein, G. Lindzey, R.D. Luce (Eds.), Stevens's Handbook of Experimental Psychology (Second edition, Vol. 1, pp. 503-546). New-York: Wiley.

Sasvàri, L. (1979). Observational learning in Great, Blue & Marsh Tits. Animal Behaviour, 27, 767-771.

Sasvàri, L. (1985a). Different observational learning capacity in juvenile and adult individuals of congeneric bird species. Zeitschrift für Tierpsychologie, 69, 293-304.

Sasvàri, L. (1985b). Keypeck conditioning with reinforcements in two different locations in thrush, tit and sparrow species. Behavioural Processes, 11, 245-252.

Seligman, M.E.P. (1970). On the generality of the laws of learning. Psychological Review, 77, 406-418.

Sherry, D.F. (1985). Food storage by birds and animals. Advances in the study of behavior, 15, 153-188.

Sherry, D.F. & Schacter, D.L. (1987). The evolution of multiple memory systems. Psychological Review, 94, 439-454.

Sherry, D.F., Vaccarino A.L., Buckenham, K. & Herz, R.S. (1989). The hippocampal complex of food-storing birds. Brain, Behavior, and Evolution, 34, 308-317.

Shettleworth, S.J. (1972). Constraints on learning. Advances in the study of behavior, 4, 1-68.

Shettleworth, S.J. (1990). Spatial memory in food-storing birds. Philosophical Transactions of the Royal Society of London, Series B, 329, 143-151.

Shettleworth, S.J. (1993) Where is the comparison in comparative cognition? Alternative research programs. Psychological Science, 4, 179-184.

Strupp, B.J. & Levitsky, D.E. (1984). Social transmission of food preferences in adult hooded rats (Rattus norvegicus). Journal of Comparative Psychology, 98, 257-266.

Thorndike, E.L. (1911). Animal Intelligence. New York: Hafner.

Todt, D.H., Hultsch, H. & Heike, D. (1979). *Conditions affecting song acquisition in* nightingales (Luscinia megarhynochos). Zeitschrift für Tierpsychologie, 51, 23-35.

Vander Wall, S.B. & Balda, R.P. (1977). Coadaptations of the Clark's nutcracker and Pinon pine for efficient seed harvest and dispersal. Ecological Monographs, 47, 89-111.

Veissier, I. (1993). Observational learning in cattle. Applied Animal Behaviour Science, 35, 235-243.

Vieth. W., Curio, E., & Ernst, U. (1980). The adaptive significance of avian mobbing. III. Cultural transmission of enemy recognition in blackbirds. Cross-species tutoring and properties of learning. Animal Behaviour, 28, 1217-1229.

Ward, P. & Zahavi, A. (1973). The importance of certain assemblages of birds as "information centers" for food finding. Ibis, 115, 517-534.

Whiten, A. and Ham R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. Advances in the Study of Behaviour, 21, 239-283.

Wilkinson, L. (1989). SYSTAT: The System for Statistics. Evanston, IL: SYSTAT, Inc.

Wyles, J. S., Kunkel, J. G. & Wilson, A. C. (1983). Birds, behavior and anatomical evolution. Proceedings of the National Academy of Science (USA), 80, 4394-4397.

Figure 1: Comparisons of foraging behaviour

(modified from Redman 1995)

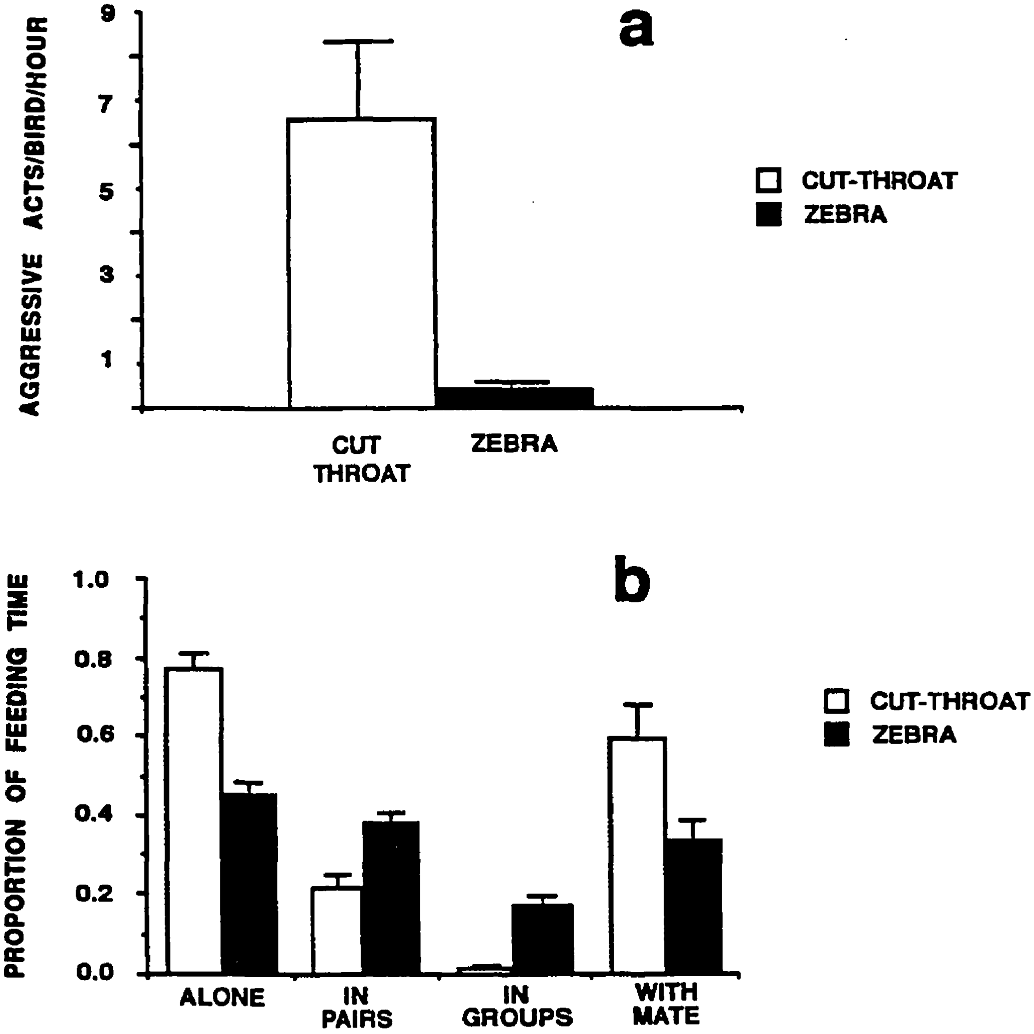


Figure 1a: mean rate of aggression (number of aggressive acts/indivdual/hour)

Figure 1b: mean proportion of foraging time spent alone, in pairs, in groups, and proportion of cases in which the pairs in column two were mates

Figure 2: spatial arrangement of the apparati

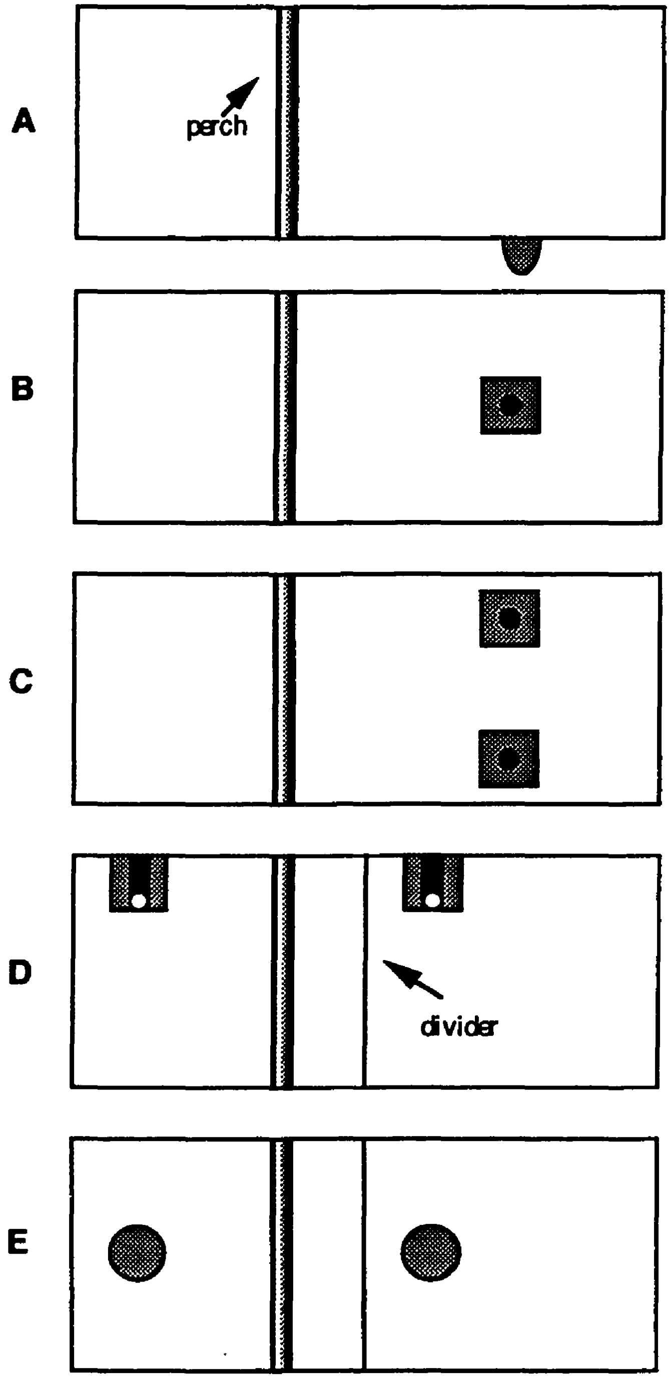


Figure 2: spatial arrangements of the feeders in each of the tests of learning/performance: 2a - neophobia (NEO1A, NEO1B); 2b - neophobia and general learning (NEO2A, NEO2B, GEN1); 2c - general learning (GEN2); 2d - social learning (SOC1); 2e - social learning (SOC2)

Figure 3: details of the apparati

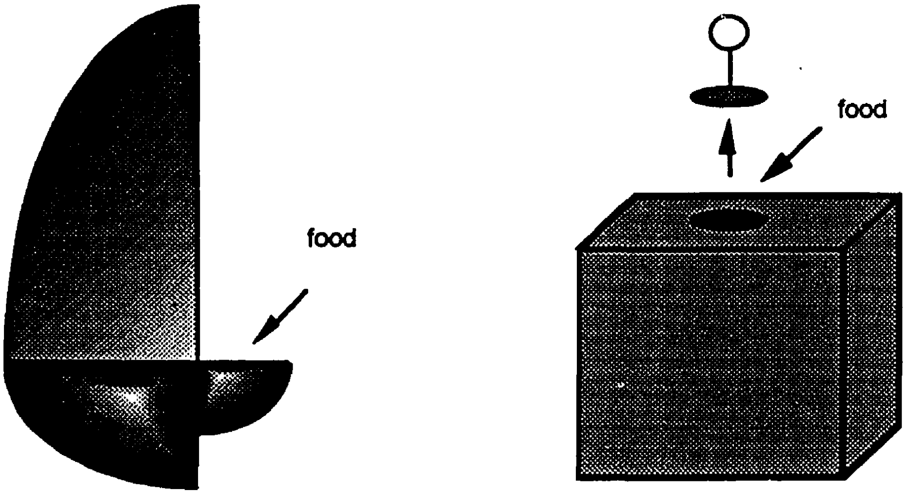


FIG. 3a: COMMERCIAL FEEDER

FIG. 3b: BLACK CUBE

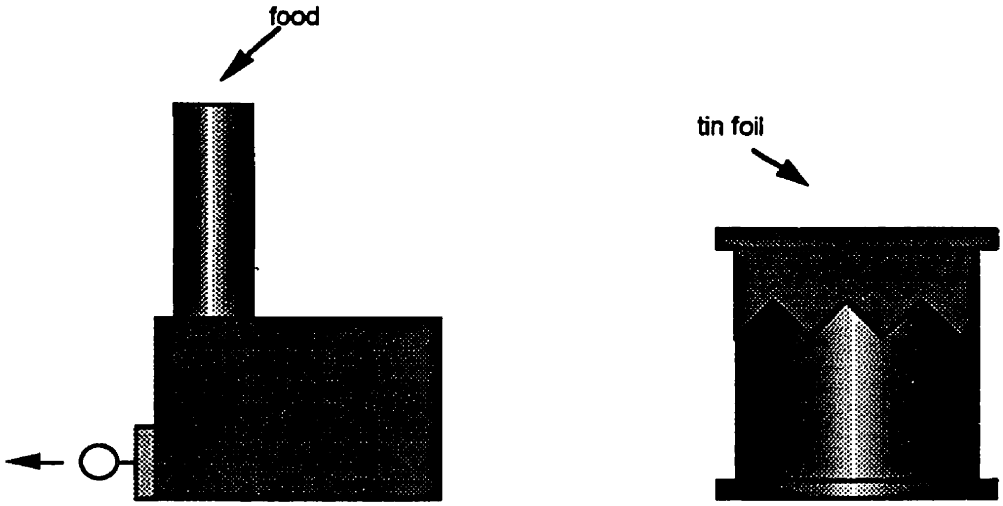


FIG. 3c: TUBE FEEDER

FIG 3d: FOIL COVERED JAR

Figure 3: feeders used in the various tests of learning/performance: 3a - tests of neophobia; 3b - neophobia and the tests of general learning; 3c and 3d - tests of social learning.

Figure 4: mean scores on tests of learning/performance

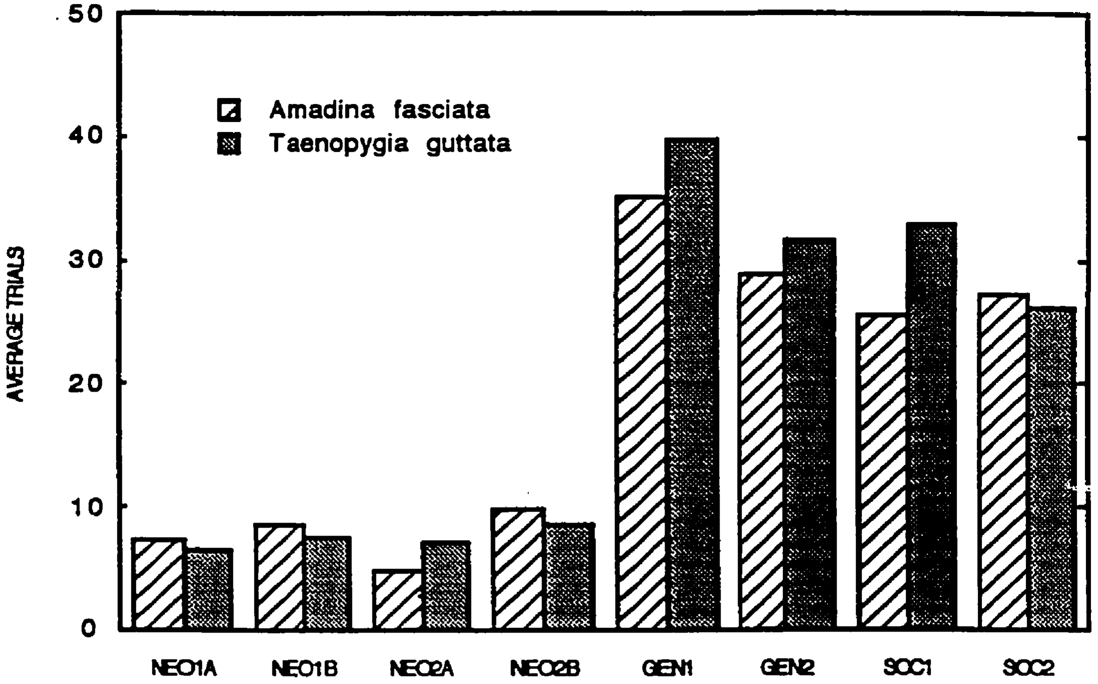


Figure 4: average trials to criterion for each species on each task. Neophobia tasks: NEO1A to NEO 2B; general learning tasks: GEN1 and GEN2; social learning tasks: SOC1 and SOC2.

Figure 5: frequency distributions of correlation coefficients between control and adaptive tests of learning/performance

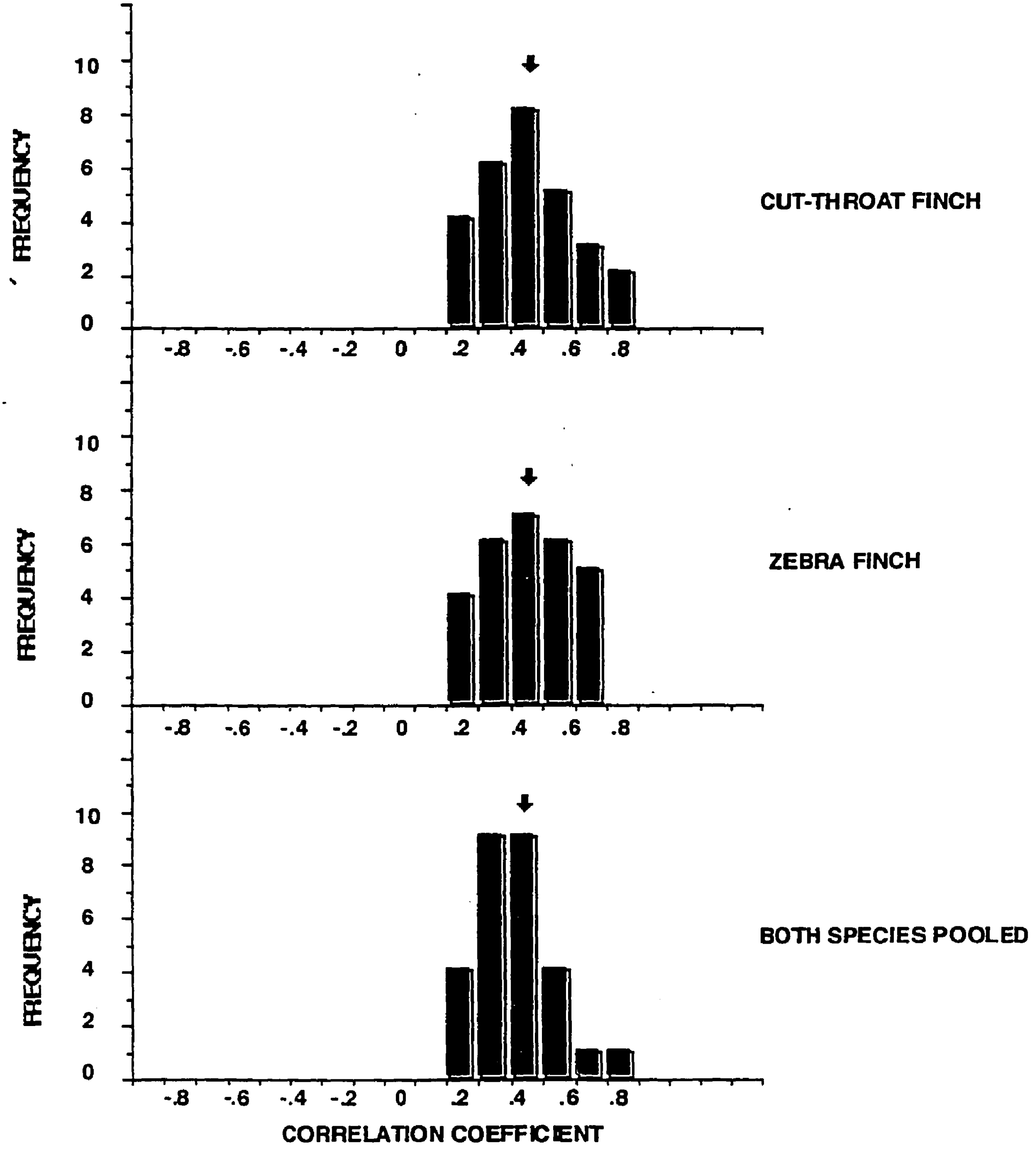


Table 1

Trials to criterion for each subject on the 8 tasks for *Amadina fasciata*

			Amadina Fasciata		(cut-throat)			
Bird	NEO1A	NEO1B	NEO2A	NEO2B	GEN1	GEN2	SOC1	SOC2
1	4	12	3	6	45	25	39	56
2	6	11	8	10	50	29	45	40
3	14	3	4	14	22	27	36	3
4	12	20	12	5	37	31	39	18
5	1	5	1	4	36	30	20	35
6	17	12	1	15	34	22	30	20
7	6	9	3	16	27	20	35	31
8	10	6	9	19	55	33	13	34
9	6	2	3	11	45	18	22	X
10	1	5	3	3	12	19	T	T
11	4	8	1	10	19	15	7	11
12	6	3	3	2	31	19	29	41
13	8	11	11	17	54	44	37	12
14	5	10	8	6	40	38	18	31
15	9	6	1	12	48	43	25	38
16	1	10	9	7	42	22	3	8
17	7	4	2	18	33	26	19	48
18	13	14	1	1	33	30	23	13
19	11	17	13	19	21	55	35	40
20	4	4	1	1	17	31	11	13
mean:	**7.3**	**8.6**	**4.9**	**9.8**	**35.1**	**28.9**	**25.6**	**27.3**

T-initial tutor
X-deceased

Table 2

Trials to criterion for each subject on the 8 tasks for *Taenopygia guttata*.

			Taenopygia guttata		(zebra)			
Bird	NEO1A	NEO1B	NEO2A	NEO2B	GEN1	GEN2	SOC1	SOC2
1	16	11	7	14	53	43	49	22
2	13	1	9	9	49	26	17	38
3	12	17	10	14	28	22	40	20
4	10	15	7	10	38	31	36	12
5	13	8	1	13	57	30	45	51
6	2	9	23	8	34	41	38	10
7	3	11	4	9	27	34	22	X
8	6	6	7	9	30	21	14	X
9	8	7	8	4	44	37	51	X
10	3	3	1	5	21	19	T	T
11	4	7	1	11	46	35	47	25
12	1	10	9	9	40	42	44	37
13	5	1	12	6	34	46	22	46
14	1	4	7	15	49	39	38	33
15	1	6	1	6	24	22	9	17
16	6	7	4	3	35	21	37	10
17	4	3	1	1	59	30	11	9
18	2	2	8	8	52	37	45	23
19	15	11	14	13	34	41	34	35
20	4	12	7	6	43	16	23	31
mean:	**6.45**	**7.55**	**7.05**	**8.65**	**39.85**	**31.65**	**32.74**	**26.19**

T-initial tutor
X-deceased

Matrix of correlation coefficients between tasks

	neo1b	neo2a	neo2b	gen1	gen2	soc1	soc2
CUT-THROAT FINCH							
neo1a	.369	.130	.412	.079	.289	.421	.224
neo1b		.576**	.037	.123	.408	.397	.051
neo2a			.317	.330	.553*	.272	.045
neo2b				.255	.318	.190	.132
gen1					.250	.156	.292
gen2						.246	.143
soc1							.292
ZEBRA FINCH							
neo1a	.351	.104	.453*	.233	.049	.232	.227
neo1b		.184	.421	.228	.080	.314	.236
neo2a			.197	.139	.466*	.166	.009
neo2b				.117	.306	.425	.390
gen1					.312	.314	.211
gen2						.458*	.266
soc1							.098

TWO SPECIES POOLED

neo1a	.364*	.091	.418**	.133	.152	.272	.004
neo1b		.320*	.185	.057	.165	.307	.122
neo2a			.212	.120	.514**	.264	.036
neo2b				.175	.287	.228	.218
gen1					.299	.278	.237
gen2						.375*	.186
soc1							.183

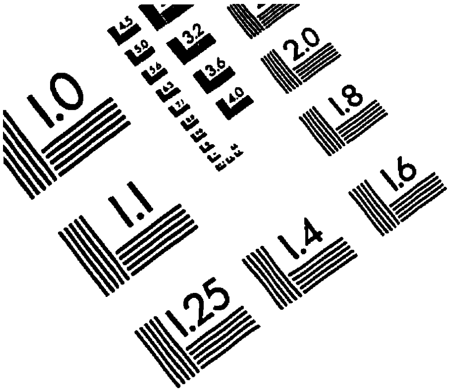
---

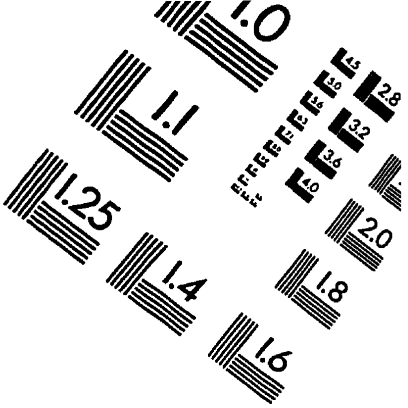
*P<0.05 **P<0.01

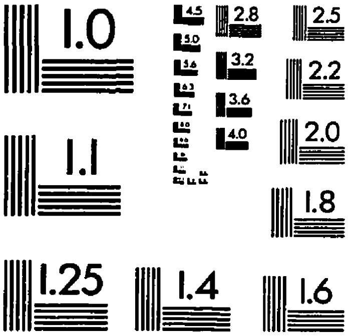
Appendix

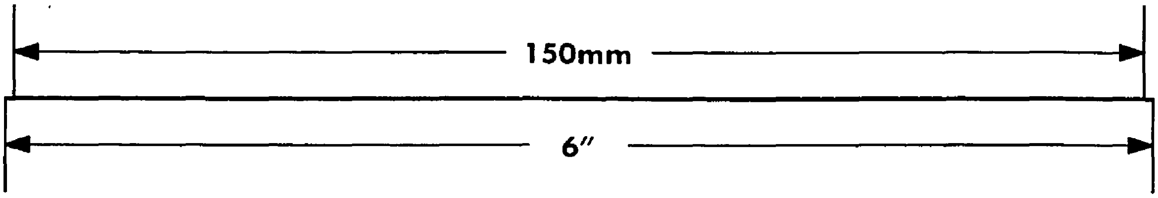
Test of the adaptive hypothesis: MANOVA summary table for the contrast:
[1 1 1 1 1 1 -3 -3] using the data in tables 1 and 2

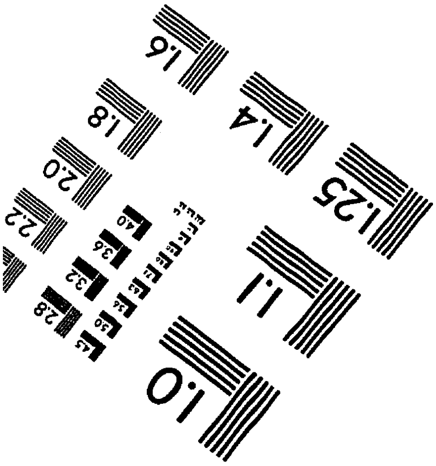
Source	Sum of Squares	d.f.	Mean Squares	F	P
contrast	1073.383	1	1073.383	0.354	0.556
error	96948.882	32	3029.653		

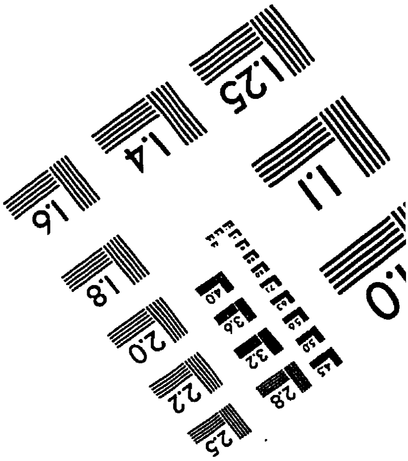












APPLIED IMAGE, Inc
1653 East Main Street
Rochester, NY 14609 USA
Phone: 716/482-0300
Fax: 716/288-5989