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THE ROLE OF INTERVENING VARIABLES IN LEARNING DIFFERENCES BETWEEN GROUP-FORAGING AND TERRITORIAL COLUMBIDS

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Abstract

Previous work on feral pigeons (*Columba livia*) and zenaida doves (*Zenaida aurita*) suggests that both individual and social learning varies with type of competition: rapid non-aggressive feeding is associated with rapid individual learning as well as rapid social learning from the tutor types a bird usually feeds with in the field. Comparative learning tests, however, may be influenced by intervening variables like neophobia and tameness: tests are always run on captive animals by human experimenters using novel stimuli.

This thesis compares pigeons to territorial and group-feeding zenaida doves on their response to novel stimuli in the field and in captivity, in the presence or absence of humans. In single cages, tameness and neophobia covary with learning: pigeons are more rapid than doves at learning, at interacting with a novel apparatus and at feeding in the absence of the human; territorial zenaida doves are slower than group-feeding doves on all three tests. Multiple regressions show that neophobia and tameness explain an important part of the variance in learning. These results are confirmed by a re-analysis of data previously obtained on finches (Whittle, 1996), where neophobia predicts individual learning which in turn predicts social learning.

In the field, however, neophobia has opposite effects: territorial zenaida doves now show the smallest effect of novel stimuli on feeding latency. Experiments that test evolutionary predictions about learning using captive animals are thus open to questions of internal and external validity: when we measure comparative performance on a captive learning test, is it really learning we are measuring and does it mirror, as it should, adjustment to environmental novelty in the field?

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Résumé

Des travaux antérieurs sur les pigeons bisets (*Columba livia*) et les tourterelles à queue carrée (*Zenaida aurita*) suggèrent que l'apprentissage individuel et social sont associés avec la compétition alimentaire nonagressive: ce mode de compétition covarie avec la vitesse de l'apprentissage individuel, de même qu'avec l'apprentissage par observation de tuteurs issus de l'espèce la plus abondante dans les aggrégations sur le terrain. Les épreuves comparatives d'apprentissage peuvent cependant être influencées par des variables intervenantes comme la néophobie et la familiarité avec les humains, car ces épreuves impliquent toujours un contact avec des stimuli nouveaux et un expérimentateur.

Cette thèse compare des pigeons bisets avec des tourterelles territoriales et grégaires sur leur réponse aux stimuli nouveaux sur le terrain et en captivité, avec ou sans expérimentateur visible. Quand les oiseaux sont étudiés seuls en cage, la néophobie et la latence d'alimentation covarient avec l'apprentissage: les pigeons apprennent plus vite que les tourterelles grégaires et mangent plus vite que ces dernières dans un appareil nouveau (néophobie) et dans un godet familier en l'absence de l'expérimentateur. Les tourterelles territoriales sont par ailleurs plus lentes que les tourterelles grégaires sur l'ensemble des trois épreuves. Des régressions multiples montrent que la néophobie et la latence d'alimentation prédisent une part importante de la variance dans l'apprentissage. Ces résultats sont confirmés par une réanalyse des données recueillies par Whittle (1996) sur deux espèces de pinsons, où la néophobie prédit l'apprentissage individuel et celui-ci prédit en retour l'apprentissage social.

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Sur le terrain, la néophobie a des effets opposés: les tourterelles territoriales ont maintenant la latence la plus courte d'alimentation en présence d'un objet nouveau et les pigeons la latence la plus longue. Les expériences en captivité sur des prédictions évolutives concernant l'apprentissage sont donc sujettes à des problèmes de validité interne et externe: quand nous mesurons la performance relative de deux ou plusieurs types d'animaux dans un test d'apprentissage en captivité, est-ce vraiment l'apprentissage que nous estimons? Et cette performance reflète-t-elle, comme elle le devrait, la réponse des animaux à des situations nouvelles sur le terrain?

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Preface

Remarks on traditional and manuscript-based theses As required by the Guidelines for Thesis Preparation, the following article is quoted:

"Candidates have the option of including, as part of the thesis, the text of one or more papers submitted for publication, or the clearly-duplicated text of one or more published papers. These texts must by bound as an integral part of the thesis.

If this option is chosen, connecting texts that provide logical bridges between the different papers are mandatory. The thesis must be written in such a way that it is more than a mere collection of manuscripts; in other words, results of a series of papers must be integrated.

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

Additional material must be provided where appropiate (e.g. in appendices) and in sufficient detail to allow a clear and precise judgement to be made of the importance and originality of the research reported in the thesis.

In the case of manuscripts co-authored by the candidate and others, the candidate is required to make an explicit statement in the thesis as to who contributed to such work and to what extent. Supervisors must attest to the accuracy of such statements at the doctoral oral defense. Since the task of the examiners is made more difficult in these cases, it is in the candidate's interest to make perfectly clear the responsibilities of all the authors of the co-authored papers."

Special Note

This thesis is partly based on a manuscript to be submitted for publication. The co-authors of the paper will be Erika Marzinotto and Louis Lefebvre. I will be first author of the paper. I am solely responsible for the planning and design of all experiments in this thesis. I am further solely responsible for animal maintenance, data collection and analysis of part a of chapter 2. Erika Marzinotto did the actual data collection for the field experiment described in part b of chapter 2; I was responsible, however, for planning and supervising these experiments in the field.

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Chapter 1

General Introduction

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Comparative Studies of Learning

When learning is compared between species with different natural histories, two different outcomes are predicted by two different theories. General process theory predicts that all instances of associative learning involve the same basic mechanisms and processes (Roper, 1983). Adaptive specialization theory, also referred to as the ecological program (Shettleworth, 1993) or adaptive/evolutionary framework (Rozin & Schull, 1988), predicts that natural selection should cause animals with different environmental demands to show differences in specialized learning abilities (Rozin & Kalat, 1971; Sherry & Schacter, 1987).

The strongest support for the ecological approach is provided by comparative experiments on spatial memory, filial imprinting and song imitation. Birds which cache food have a better spatial memory than those that do not (Balda & Kamil, 1989) and also possess a larger hippocampus, a structure that is known to be associated with spatial learning (Sherry et al., 1989; Krebs et al., 1990). A similar relationship between spatial memory (specifically food storing, homing and home range size) and relative hippocampus size has also been found in a variety of birds and mammals (reviewed by Sherry et al, 1992), such as polygynous male voles (Gaulin & FitzGerald, 1989), kangaroo rats (Jacobs, 1992) and homing pigeons (Bingham et al., 1990).

Filial imprinting has long been known to co-vary with precocial (as opposed to altricial) development. Its neural basis appears to be the left side of the intermediate and medial part of the hyperstriatum ventrale (IMHV; reviewed by Horn, 1990). Vocal imitation is linked to the production of complex song in most oscines, but not in non-

passerines, brood parasites (West & King, 1996) or songbirds with low site fidelity (Kroodsma & Verner, 1978). The neural basis of vocal imitation appears to be the high vocal centre (HVC; Nottebohm et al, 1990), which shows strong sexual dimorphism in oscine species where song is also dimorphic (Brenowitz & Kroodsma, 1996).

Social learning, the modification of behaviour following observation of others, can also be seen in ecological terms (Lefebvre & Palameta, 1988). Historically, it is on this type of learning that ecological predictions were first proposed (Klopfer, 1959, 1961). Klopfer made two important comparative predictions: (1) when comparing solitary species to group-living ones, the social learning ability of the former should be lower; (2) opportunistic species should have more or different social learning abilities when compared to conservative ones. Klopfer (1961) provided the first set of empirical data testing these predictions; he found that the great tit, a more opportunistic bird, was better at learning an avoidance response in the presence of a conspecific than the more conservative greenfinch. Sasvari (1979, 1985a, b) confirmed Klopfer's predictions by correlating social learning differences between great tits, blue tits, marsh tits, blackbirds and song thrushes with differences in opportunism. In a comparison between mandrills, baboons and vervet monkeys, Cambefort (1981) and Jouventin et al. (1976) found that social learning ability varied with the complexity of the group structure in these primates. At first glance, the evidence thus suggests that social learning is an adaptive specialization to gregarious and opportunistic lifestyles. Closer examination of these comparative tests raises several problems, however.

Confounding Versus Intervening Variables

The major problem that has plagued comparative studies of learning is that confounding variables, rather than differences in ecologically-specialized learning abilities, may be responsible for interspecific differences in performance. MacPhail (1982, 1985) was the first to point out that contextual variables could bias comparative learning tests. He recognized that different species may respond in different ways to the stimulus, motivational and reinforcement characteristics of the learning task, leading to spurious differences in the outcome. After an extensive review of the cases published up to the time of his critique, MacPhail (1982) concluded that no comparative study had ever demonstrated a difference in learning or cognition that could not be attributed to contextual variables.

Confounding or contextual variables can be described as unavoidable co-variates that may cause comparative differences the experimenter will wrongly attribute to learning. Confounding variables are theoretical nuisances that need to be eliminated to discover what is really going on. Several authors in the comparative literature have proposed ways to achieve this elimination (see review below). Elimination of learning co-variates is also a basic premise of all noncomparative work in learning psychology: in traditional, general process approaches to animal learning, pre-experimental taming and habituation of subjects to study conditions and apparati is a routine procedure, whose goal is to minimize the role these variables could play in learning processes.

This thesis is based on a very different view: co-variates of learning are not seen as confounds that must be eliminated, but as intervening variables whose theoretical role deserves to be investigated. The design, statistics and interpretation used in this thesis all focus on the view that variables like neophobia and tameness around humans may be at the very base of both inter-specific, interpopulation and inter-individual differences in learning. In this role, neophobia and tameness are two key variables in a set of related traits that may be associated with the ecology of learning and cognition (Lefebvre, 1998).

Neophobia and tameness could have a pervasive role in comparative learning tests. These tests routinely predict a difference in latency, errors or retention time between types of animals (usually species) that show differences in natural history that would logically create selective pressures for the learning. To test this prediction, we have human experimenters conducting experiments in captivity, experiments that involve interacting with a novel apparatus and solving a feeding problem, usually motivated by food deprivation. If the animals show the predicted effect on the learning criterion, we conclude that our hypothesis is supported. Yet the differences in learning could be strongly affected, if not entirely caused, by intervening variables such as captivity, testing by a human, the apparatus as a novel or meaningful stimulus, response to food deprivation or some other unobserved learning ability.

Neophobia, the fear of novelty, is one of these potential intervening variables. Greenberg (1983, 1984, 1989, 1990) studied two species of warblers (*Dendroica castanea* and *D. pensylvanica*) and two species of sparrows (*Melospiza melodia* and *M. georgiana*) and found differences in their levels of neophobia both in the field and in captivity;

these patterns correlate with differences in opportunism between the species. In the wild, both warbler species usually glean insects off foliage; however, *D. castanea* is the more generalist of the two as it feeds on a wider and more diverse range of substrate types than *D. pensylvanica. D. castanea* is also more opportunistic, venturing out of the forest and into human habitats, feeding on lawns and in garbage cans (Greenberg, 1984). The song sparrow (*M. melodia*) also exploits human habitats and is more general in its range of colonised habitats than the swamp sparrow (*M. georgiana*), which occurs mainly in marsh land (Greenberg, 1989). Greenberg (1990) related both opportunism and neophobia to the degree of exploration an individual will undertake. For example, if an animal has a low level of neophobia, it follows that it will be more likely to explore and exploit new situations.

In the accompanying learning experiments, Greenberg observed that once differences in neophobia are eliminated through pre-test habituation to the learning apparatus, ecologically predicted learning differences between the more opportunist-generalist and the more conservative-specialist of the species are not found. In eliminating the initial difference in neophobia between his species, Greenberg adopted the confounding variable approach outlined above; this prevented the spurious effect of neophobia on learning, but contrary to the approach I will use in this thesis, it did not allow a teasing apart of the relative proportion of learning variance accounted for by the ecological difference and by neophobia.

A further study that considered the confounding effect of neophobia is that of Daly et al (1982). These authors found differences in both neophobia and learning between a more generalized species of kangaroo rat (*Dipodomys merriami*) and a more specialized one (*D. microps*). As in Greenberg's work, differences in taste aversion learning between the two species could be accounted for by their initial differences in neophobia to the novel foods used in the aversion learning procedure; unlike Greenberg, Daly et al (1982) did not strive to eliminate neophobia before their learning experiment, but only invoked the parallel differences in the two tests *a posteriori* in their discussion to caution their readers in interpreting the apparent learning difference in terms of specialized effects of diet.

Tameness in the presence of humans may be another important variable in comparative learning tests. Generalist-opportunist species often exploit habitats that are modified by human activity. Contrary to conservative species, this brings them into frequent contact with humans. Since comparative learning tests involve capture (or rearing in the case of subjects that are not wild-caught), handling and testing by humans, this difference in tendency to tolerate closeness to humans may also be a major factor. Surprisingly, the subject of tameness has received very little attention in the literature (Lefebvre, 1996). In relation to opportunism, tameness implies that a species will be less stressed by captivity and handling in the laboratory and more adaptable to anthropogenic changes in its environment, such as urbanization. Thus, the relative performance of the species tested may partially reflect its tolerance of humans rather than a superior ability on the learning test being used.

Approaches to Eliminating Confounding Variables

Several authors have realized that comparative tests of learning may be difficult to interpret and have proposed methods to cope with these problems. The traditional approach proposed by Bitterman (1975) entails systematic variation of the confounding factors. A constant interspecific pattern of performance throughout multiple tests for different learning abilities suggests that the confounding variables cannot account for the comparative effects found. This method of systematic variation succeeds in altering relative performances enough to highlight a contextual variable, but it does not completely eliminate the differences (Bitterman, 1975; MacPhail, 1982). A more fundamental problem with Bitterman's (1975) work is that he works from a "scala naturae" perspective, applying his theories to very distantly related taxa like insects, fish and mammals; his results consequently reflect the "increasing" sophistication of learning mechanisms as one moves from "simple" to "complex" animals (see Riddell et al. 1976, for a critique of this approach). Although obvious coherent differences are found on different types of tests, the results tell us only about phyletic constraints and little about the effects of selection. To avoid this problem, adaptive effects on learning should only be tested on taxonomically close species (Domjan & Galef, 1983).

Kamil (1988) suggested an alternative to the traditional approach that involved a battery of learning tests which measure the same learning ability. By varying procedural details so that different contextual variables are exposed, the confounding variables are eliminated due to quantitative variation having no effect on relative performance. In line with the ecological hypothesis, it is thought that

the more specialized species will outperform the other species on all tests. Unfortunately, Kamil's approach may be incapable of controlling for confounding variables such as neophobia or tameness, which have a common effect across all tests (Whittle, 1996).

The baseline comparison (Hilton & Krebs, 1990; Shettleworth, 1993) matches species on learning abilities unrelated to the adaptive hypothesis. Thus an adaptive specialization is presumed when the specialized species outperform the other species on the adaptive test but demonstrate the same performance on the baseline test. This approach is similar to the one used in studies that interfere with a given ability, either by lesioning its neural basis (Sherry et al, 1989) or mutating its genetic one (Silva et al 1996); in such cases, the effect of the interference must be shown to be specific to the ability being tested. In spatial memory, the routine control for specificity of interference is to contrast the predicted deficit in a landmark use task (e.g. the Morris water maze) with normal performance in an orientation problem that is not based on landmark learning. In comparative learning tests, it is surprising that such baseline controls are not as systematically performed as they are in genetic or neural interference work.

Despite its obvious value, the baseline control technique can sometimes be too conservative. For example, it may lead to type 2 error when species differ in the same direction in both control and experimental prediction tasks (Lefebvre 1996). Lefebvre & Giraldeau (1996) have proposed an alternative logic based on the allometric approach used in comparative biology: for traits predicted to differ adaptively (for instance, size of the hippocampus) due to a divergent selective context (for instance, scatter hoarding in a highly seasonal

alpine habitat), hypotheses are not tested on absolute trait size, nor is it required that the compared species be identical on some baseline control (for instance, body weight). Comparative biologists simply use the residual deviation of the predicted trait on other confounding traits in their test of the hypothesis: it is relative hippocampus size, regressed against body weight or size of the rest of the telencephalon (Sherry et al 1989; Krebs et al 1989) that is predicted to be larger in scatter hoarders.

Following this logic, Lefebvre and Giraldeau (1996) suggested two statistical procedures that control for the effects of confounding variables in comparative tests of learning: (1) linear regressions, using the deviation from the confidence limits of a control task regression to test for significance of the result on the adaptive task, and (2) speciesby-task interaction in an analysis of variance. Lefebvre & Giraldeau (1996) argued that the focus of comparative tests should be on the difference between control tasks and adaptive ones, rather than on absolute differences between species. Using these procedures on data from Sasvari (1985a, b) and Klopfer (1961), Lefebvre & Giraldeau (1996) found little comparative evidence to suggest that social learning is an adaptive specialization to opportunism and/or group-living, and concluded instead that the ecological variables tested were probably associated with interspecific differences in both individual and social learning.

Shettleworth and Hampton (1996) highlighted a conceptual problem with Lefebvre and Giraldeau's (1996) regression approach, in that it assumes an analogy between cognition and allometry. They liken the basic body size co-variate of allometry to a general intelligence factor, which would have as pervasive an effect on cognitive abilities as size has on all anatomical traits. Since general intelligence is no longer an importantconcept in cognitive psychology, Shettleworth & Hampton (1996) argue that the analogy between allometry and cognition has no heuristic value.

A fourth procedure, possibly the most interesting one when it can be applied, has been suggested by Balda et al (1996) and Bednekoff & Balda (1996a, b). These authors reasoned that in cases where closelyrelated species show opposite differences in two or more features of their natural history, it is highly unlikely that the predicted opposite differences in learning abilities would be spurious. Bednekoff & Balda (1996a, b) apply this idea to three seed caching corvid species: Clark's nutcracker (Nucifraga columbiana), Pinyon Jays (Gymnorhinus cyanocephalus) and Mexican Jays (Aphelocoma ultramarina), that differ in environmental conditions, reliance on seed caching and social organization. These differences are predicted to have opposite effects on spatial and social learning tasks. All three species inhabit different elevations, experiencing different ranges of climatic conditions, and thus developing differential dependency on previously cached food for reproduction and survival during the winter. Clark's nutcrackers have a simple social structure, living in harsh climatic conditions (elevations of 2200 to 3200m; winter conditions: deep snow, overcast skies and cold temperatures), being reliant for 80 to 100 percent of their winter diet on previously cached food sources. Pinyon jays, like nutcrackers, also live in harsh climatic conditions (elevations of 1850-2200 m) and rely on cached food for 70 to 90 percent of their winter diet; however, pinyon jays live in a very complex social structure.

Mexican jays also live in a complex society but experience relatively mild climatic conditions (elevations of 1650-2200 m) and, as a result, are less reliant on previously hidden food sources relative to the other two corvid species (reviewed by Balda et al., 1996).

These ecological differences led Balda et al. (1996) to predict that species which are more reliant on remembering hidden sources of food (nutcrackers and pinyon jays) should be able to recover hidden caches more accurately than those that have other dietary alternatives (mexican jays). This prediction is supported by captive experiments (Balda & Kamil, 1989; Bednekoff et al. 1997). Balda et al. (1996) further showed that these apparent species differences in cognitive ability were not due to non-cognitive contextual variables (Bitterman, 1975). They used the multiple experimental task procedure advocated by Kamil (1988), employing a battery of spatial, non-spatial and control tasks to measure the cognitive ability of their corvid species. In spatial memory experiments, it was found that performance relates strongly to degree of dependence on stored food: nutcrackers performed better than pinyon jays who, in turn, performed better than mexican jays.

When the three species were given a social task, however, their relative performance was different from that obtained in spatial tests: pinyon jays were better than mexican jays at remembering the location where they saw a conspecific hide food, while Clark's nutcracker were the poorest of the three. This relative performance is consistent with species differences in sociality. Social and spatial tasks thus reveal opposite differences in the three species, which correlate with opposite social and caching specializations. Balda et al. (1996) interpret these results as evidence for two separate learning specializations, one

social and one spatial. This interpretation is different from the rest of the social learning literature, however, which suggests that social learning is a non-specialized variant of individual learning (Lefebvre & Giraldeau 1996; Heyes 1998). A closer look at the results from Balda & Kamil's group suggests, however, that this conclusion may be premature. Olson et al (1995) have conducted control experiments on the three corvid species studied earlier. In these tests, which involve a non-spatial, non-social type of visual discrimination learning, the three species showed the same relative difference in learning speed that they did in Bednekoff and Balda's (1996a) social experiment; the control task performance is thus different from the spatial one, but not from the social one, suggesting, as the rest of the literature does, that spatial learning is specialized, but that social learning is not. This conclusion is similar to the one reached by Lefebvre & Giraldeau (1996) in re-analyzing the learning literature in another food caching group, the family Paridae. Among Paridae, the marsh tit caches food, while the great tit does not: results from comparative tests (Hilton & Krebs, 1990) show that marsh tits are better at spatial learning than are great tits, a finding that ranks the two species in the opposite order they rank in both the social and non-social variants of Sasvari's (1979, 1985a, b) experiments. As with corvids, the parid literature thus suggests a specialisation for spatial memory, but a common pattern of interspecific variation for social and individual learning.

A final approach to the elimination of confounding variables is provided by Whittle (1996). Whittle (1996) conducted a comparative study on 2 species of grassfinches, *Amadina fasciata* and *Taenopygia guttata*. These finches are similar morphologically and behaviourally but

employ varying degrees of scramble (non-aggressive) and interference (aggressive) competition in their foraging strategy. T. guttata. uses scramble competition to a greater extent than does A. fasciata, who often uses interference competition as a form of defense against feeding conspecifics (Redman, 1995). Using multivariate analysis of variance (manova) and a battery of neophobia, individual and social learning tests, Whittle (1996) was able to focus on between group differences in social learning, factoring out neophobia and individual learning tests as a single canonical variable. Unfortunately, despite differences in feeding competition (Redman, 1995), the two finch species did not differ in any of the tests given. Whittle (1996) concluded that his data showed no specialized effect of competition mode on social learning, once all other co-variates have been factored out. The value of his work is difficult to judge, however, due to three problems: (i) the lack of interspecific differences on any of the neophobia and learning tests could be responsible for the negative effects of the manova; (ii) the multivariate technique itself imposes a particular statistical model that may or may not be appropriate. Instead of creating a single canonical variable from the co-variance in the control tasks, it may be better to include the controls separately and to see if each of them can predict the outcome of learning; (iii) the manova focuses only on between group differences; an approach that could simultaneously look at inter-group and inter-individual variation, as the present thesis will do, may be more discriminating.

Internal and External Validity of Comparative Learning Tests

Whenever a controlled test is used to measure a given hypothetical ability, two important concepts must be examined: the external and the internal validity of the test. We must first be sure that performance on the test reliably reflects the ability we want to measure, not response to the tester or performance on that particular test day. This is why we estimate the internal validity of a test. Many of the contextual controls for confounding variables are examples of internal validity procedures. The search for intervening variables that will be a primary focus of this thesis also falls within the category of internal validity tests: determining for a comparative experiment the importance of tameness in front of a human experimenter is analogous, for instance, to measuring the sensitivity of an IQ test in humans to identity or gender of the tester.

The second feature that must be assessed is external validity: we must be sure that a controlled test actually measures its target ability as the latter operates in natural situations. In an IQ test in humans, for instance, we want to know whether a limited set of written questions validly assesses intelligence as it is used in scholastic or every day situations. In a comparative test with animals, we want to know whether the test adequately measures a learning ability as it is used in the field. Shettleworth and Krebs (1986) have discussed this issue at length for spatial memory, developing a "window shopping" procedure that is both ecologically valid for food cachers and not trivially inconclusive for non-cachers.

In most contemporary comparative work, the ecological or external validity of a captive test is taken for granted and not

assessed experimentally. The only animal study where this assessment has been done is that of Greenberg (1989, 1990) on *Melospiza* sparrows. Greenberg performed neophobia experiments on two species of sparrows (*Melospiza melodia* and *M. georgiana*) in captivity and in the wild; the two species showed the same relative difference in the two situations, a difference that also paralleled their differences in ecological and dietary generalism. In *Melospiza* spp, therefore, the captive test is externally valid, since its results reflect species differences to novel feeding situations in the field.

This double focus on internal and external validity of learning tests will be a major focus of my thesis. In Part A of the empirical study, I will use a neophobia task in captivity to assess the role of this potential intervening variable in learning differences of wild-caught columbids tested alone in a cage. Single cage testing is a standard feature of comparative learning experiments. Its major function is to provide statistically independent data points to test adaptive predictions between group means, while removing the subjects from as many distracting sources of stimulation, be they social or physical, that could bias learning.

In using this procedure with gregarious birds, however, it is conceivable that one introduces an element of stress linked to social isolation. More importantly, response to novel situations may be very different for a group-living bird when it is obliged to be alone in a cage and when it is with other flock members in the field. One of the major advantages of group living is thought to be vigilance in risky situations. When faced with new stimuli whose risk potential is as yet unknown, gregarious animals may respond as a group; pigeons, for example,

show species-typical flight patterns when disturbed (Goodwin, 1983). These group responses in the field may be very different from the individual responses one measures in a captive test. This is why, in part b of my thesis, a neophobia experiment will also be conducted in the field, to examine the external validity of the neophobia test used in captivity.

Learning Differences Between Pigeons and Zenaida Doves

The species that will be used for all the captive and field tests in this thesis are pigeons and zenaida doves. These species are readily available and easy to work with both in captivity and in the field and several experiments have been conducted on them in our laboratory (reviewed by Lefebvre, 1996).

In a first study, Lefebvre et al. (1996) used the territorial zenaida dove and the feral pigeon in a comparative experiment to test whether social learning may be an adaptive specialization to group-living (Klopfer, 1961). The two species belong to the same family, Columbidae. Moreover, they are both highly urbanized and opportunistic, feeding in close proximity to humans and relying on human-derived foods such as bread or grain warehouse spillage in the two environments in which they live, Barbados and Montréal. The major difference between the two species of Columbids is in their social organization: pigeons are gregarious, but most zenaida doves are territorial and solitary feeders. Lefebvre et al. (1996) found that pigeons were able to learn more rapidly than doves in both social and non-social situations and also ate more rapidly in the normal feeding test. As mentioned earlier, Lefebvre & Giraldeau (1996), in a re-analysis of these results, rejected the hypothesis that social learning is an adaptive specialization to group living: once the general species differences were accounted for via the residual approach, no specialized differences between the two species remained.

Quantitative differences between the two Columbid species were thus difficult to interpret: the two species could have differed because one, the pigeon, has a history of domestication and artificial selection, not because one is gregarious and the other territorial. To avoid this problem, Dolman et al. (1996) and Carlier & Lefebvre (1996) looked at intraspecific differences between a group-feeding and a territorial columbid. Dolman et al (1996) and Carlier & Lefebvre (1996) studied two Zenaida dove populations on the island of Barbados. The doves of St. James (StJ; those studied previously by Lefebvre et al 1996) are territorial and compete aggressively with conspecifics; they often feed, however, in non-aggressive mixed species aggregations with carib grackles (Quiscalus Ingubris), lesser-antillean bullfinches (Loxigilla noctis) and common ground doves (Columbina passerina). The other zenaida dove population is from the Deep Water Harbour (DWH) and shows a more gregarious life-style, using scramble competition with conspecifics when feeding (Dolman et al., 1996); grackles feed much less often with doves in this population, mobbing them very frequently due to the proximity of colonial roosts and nests (Lefebvre, unpub. observ.). In scramble competition, animals attempt to remove food as quickly as possible from the reach of others by ingesting or hoarding it (Clark & Mangel, 1986). This may lead to a "mental arms race" (Palameta, 1989) in which a feeding technique is learned rapidly to

decrease the temporary advantage that knowledgeable foragers have over naive ones within the group. Speed is thus the key to success in scramble competition (Dolman, 1991).

Dolman et al. (1996) conducted a social learning experiment and found that the StJ doves learned more readily from a grackle tutor and the DWH doves learned more readily from a conspecific. From this it was concluded that the mode of foraging competition used in the field is a better predictor for the direction of social learning than is species identity. More recently, Carlier & Lefebvre (1997) have provided further support for this view. They discovered an intermediate Zenaida dove population on Brandon's Beach, an area situated next to the DWH. Like doves from St-James, doves from Brandon's Beach routinely use interference competition to defend their feeding and breeding territory against conspecifics; in contrast to St-James, however, doves from Brandon's Beach occasionally feed in flocks at the nearby DWH and will non-aggressively feed in small flocks when food density is increased at Brandon's as a result of provisioning. This dual foraging experience enables them to learn equally well from a conspecific as they do from a heterospecific tutor. Genetic isolation between harbour doves and Brandon doves is highly unlikely, since there is no geographical or reproductive barrier between these extremely close sites (200 m); movement of birds between these sites has also been estimated at 4% over 6 months (Carlier & Lefebvre 1997), a rate sufficient to preclude divergence in neutral allele models of gene flow (Slatkin, 1985; Wright, 1931).

This relationship between mode of feeding competition and tutor preference is further confirmed in carib grackles, the second most important species in the opportunistic guild that forages in mixed species aggregations in Barbados. Lefebvre et al. (1997) found that grackles will learn equally well from a zenaida dove tutor as they do from a conspecific, irrespective of the technique the tutor chooses to use.

As with the interspecific difference found by Lefebvre et al. (1996), however, the inter-population difference found by Dolman et al (1996) on group-feeding vs territorial doves appears to co-vary with individual learning differences. Carlier & Lefebvre (1996) found that when individuals from the two populations of doves were tested on a task that required progressive individual learning in the absence of a tutor, the group-feeding doves from the DWH learned faster than the territorial doves from StJ. This result suggests that the co-variance between pigeons and territorial zenaida doves for social learning and learning, as well as simple feeding latency, may not be a trivial effect of domestication. It may reflect instead, as does the rest of the literature, a fundamental link between learning, both social and individual, and intervening variables like neophobia and tameness. It is this hypothesised link that my thesis will examine in the three columbids studied previously.

<u>Thesis Goals</u>

More specifically, the thesis uses a three-way comparison of gregarious feral pigeons, group-feeding zenaida doves and territorial zenaida doves; previous work has concentrated only on two-way comparisons, i.e. pigeons vs territorial doves and territorial doves vs group-feeding ones. Both of these two-way studies suggest that the more gregarious bird is better at learning, but testing all three populations together enables one to tease out species differences and social ones. Two dichotomous variables can thus be used to distinguish the three animal groups: species (pigeon vs dove) and social organization (group-feeding vs territorial). If both group-feeding pigeons and doves clearly outperform territorial doves in our tests, the social variable should explain most of the variance in our analyses. If, on the contrary, pigeons clearly outperform both group-feeding and territorial doves, then the social variable will be negligible and the species one will account for most of the variance.

This thesis also uses a novel theoretical and statistical approach. All the examples discussed above have dealt with the elimination of confounding variables in comparative learning experiments; the statistical techniques that have been used in these studies accordingly reflect this goal. In this thesis, I consider variables like neophobia and tameness to be theoretically interesting intervening variables. Consequently, I do not eliminate their effects, but assess the amount of variance they account for in inter-specific, inter-population and interindividual differences in learning. I do this with the multiple regression technique. Multiple regression analysis is a method used to relate two or more independent variables to a dependent variable and therefore allows one to predict individual variation in learning from individual variation in intervening variables as well as ecological ones. It is especially useful because the independent contribution of each of these predictors can be assessed: there may very well be an effect of species on learning or social organization on learning, but if in addition to the fact that pigeons tend to be faster than doves, and groupfeeding columbids faster than territorial ones, a bird who is less neophobic tends to learn faster, then it will be individual variation in neophobia may also be a significant predictor of individual variation in learning. Dichotomous nominal variables can easily be included in multiple regressions, allowing me to simultaneously consider the effects of intervening variables like neophobia and tameness and ones like species and social organization.

To simplify this evaluation of the intervening effects of neophobia and tameness on learning, my thesis focuses on individual learning, despite the fact that part of this introduction, as well as most previous comparative work on zenaida doves and pigeons involves social learning. This is because Dolman et al (1996) showed that for different types of doves, different tutor types are needed to get adequate social learning results. Contrary to Whittle's (1996) study, therefore, an extra variable, tutor type, would need to be added as soon as *Z. aurita* is used. To avoid this problem, my thesis concentrates only on tasks where the same procedure can be performed on pigeons, group-feeding zenaida doves and territorial zenaida doves.

The final goal of this thesis is to examine the external validity of one of the captive tests for intervening variables, neophobia. A field test with novel objects will ask whether a neophobia task conducted in captivity really reflects a columbid's normal response to novelty in the wild. As mentioned earlier, this transposition from field to captive isolation is likely to be problematic when group-living species are used, as they are in this thesis.

If captive tests of neophobia in columbids are externally valid, I predict that the relative differences between gregarious pigeons, groupfeeding zenaida doves and territorial zenaida doves should be similar on the captive test and the field test of neophobia. If comparative tests of captive columbids are an internally valid assessment of specialised learning abilities, I further predict that ecological variables, not intervening ones, will significantly account for individual differences in learning latency in pigeons, group-feeding zenaida doves and territorial doves.

CHAPTER 2

The Role of Intervening Variables in Learning Differences Between Group-Foraging and Territorial Columbids

The empirical part of this thesis involves two sets of experiments, one to examine the internal validity of comparative learning tests on columbids, one to examine external validity. Part a of this chapter deals with the former and features a series of tests run on wild-caught birds; part b of the chapter focuses on field tests of neophobia, in line with Greenberg's (1989, 1990) work on *Melospiza* spp.

PART A: CAPTIVE EXPERIMENTS

Methods

<u>Subjects</u>

Twenty-two adult feral pigeons were obtained from a commercial dealer (S. Wright, Richmond Hill, Ontario), between March and September 1997; all birds were wild-trapped on farms in the vicinity of Richmond Hill. Thirty-nine adult zenaida doves were caught in Barbados in baited walk-in traps between April and June 1997. Nineteen adult doves were caught at the Barbados Mills compound, Deep Water Harbour (DWH), in the parish of St-Michael; the remaining 20 doves were caught in coastal St-James (StJ). The DWH birds feed at a landfilled site that consists of docking, grain loading, milling and storage facilities. There is little in the way of vegetation, but as a result of transport and storage operations at the Barbados Mills Plant, doves routinely feed in homospecific flocks (mean size 60; Dolman et al 1996) on large patches of spilled grain (maize and wheat), legumes (soybeans) and commercial meal.
In contrast, the 20 doves captured from StJ inhabit an area which includes a public park, hotel and church grounds, as well as the Bellairs Research Institute of McGill University. Vegetation in this area is coastal woodland, dominated by manchineel, mahogany, casuarina and coconut trees. The area provides roosting, nesting and feeding resources that allow year-round territoriality: mated pairs of zenaida doves aggressively defend their territory against conspecifics, showing very high rates of intraspecific aggression. In addition, they often feed with little antagonistic interactions in mixed species aggregations that include carib grackles (*Quiscalus lugubris*), lesser-antillean bullfinches (*Loxigilla noctis*) and common ground doves (*Columbina passerina*; Dolman et al., 1996).

Experimental procedure

All zenaida doves were housed and tested at the Bellairs Research Institute of McGill University, St-James, Barbados, while all pigeons were housed and tested at the Department of Biology, McGill University, Montréal, Québec. Lighting in Montréal was artificial and kept at 14L:10D by an automatic timer , while lighting in Barbados was natural and followed the approximate 12.L:12D daily cycle typical of the tropics. Following capture (for doves) or transport (for pigeons), each bird was banded, weighed, housed in a 40x40x40 cm cage and allowed to feed from a commercial seed mix and drink ad libitum for 6 days; birds were in visual contact with conspecifics during this phase, but not during the experiments per se. On day 7, food was withheld for 24 hours and all birds were progressively brought down to 90% of their maximum weight; this level was maintained throughout the experimental period through adjustments in the individual's daily ration.

The testing period began when birds had reached their target deprivation weight. Each testing day, birds were transferred from the housing to the experimental room and given a 10 min habituation period before that day's session commenced. The bird was returned to the housing room after each test session and fed the appropriate quantity of commercial mixed seed.

Each subject went through 3 tests in the same order: tameness, neophobia and learning. No randomization or counterbalancing of test order was done to avoid spurious negative correlation's between test results: Beauchamp (1994) has shown that poor performance on the first test given in a series, followed by habituation-enhanced performance on subsequent tests, leads to artifactually negative associations between tests. In the tameness test, food (20 g of mixed seed) was presented to the birds in its usual feeding dish over a time period of 4 consecutive days, with a maximum of 8 trials per day. All trials lasted for 2 min, with a 30 sec inter-trial-interval during which the dish containing the food was withdrawn. On days 1 and 3, the experimenter was visible to the birds throughout the entire set of trials, whereas on days 2 and 4, the experimenter was hidden behind a screen. The number of trials required before the bird fed was recorded in each daily session.

The second test, neophobia, was conducted over 5 consecutive days, with a maximum of 8 trials per day. The experimenter was hidden behind a screen during all trials. On each trial, food (2 g of mixed seed) was presented in a new apparatus, an opaque plexiglas box measuring 5.5 x 5.5 x 5 cm (Carlier and Lefebvre 1996; Hatch and Lefebvre 1997). Food was available in this apparatus in a small circular depression (1 cm deep and 1.5 cm in diameter) on the upper surface; it was easily visible and accessible and the animal therefore simply needed to approach the novel apparatus. As for the tameness test, the number of 2 min trials required by the bird before it fed from the new apparatus was recorded.

The third and final test used the same apparatus as the neophobia experiment, but the animal was required to learn a new response to open a hidden feeder (Carlier and Lefebvre 1996; Hatch and Lefebvre 1997). In this test, food was enclosed in a 5.5 x 5.5 x 1.5 cm drawer fitted with a metal ring; when pulled, the ring gave access to a 1 cm deep and 1.5 cm in diameter depression in the drawer which contained 2 g of mixed seed. Because the food was hidden and ring-pulling is an extremely low probability behaviour for columbids, each bird was run through a series of 4 successive steps in the task (modified from the 9 steps used by Carlier and Lefebvre 1996); each step differed in position of the drawer, ease of access to the seed and the behaviour needed to acquire the seed (Table 1).

Each bird was first started at level 1 and graduated to the next level of difficulty if it consumed seed in 2 trials; the lowest possible number of trials needed to reach level 4 was thus 4. The maximum number of trials given was 40, at a rate of 8 trials per day over 5 consecutive days; the highest possible latency was thus 41 trials at level 1 (i.e. the 40 trials + 1, to distinguish a bird that failed from a bird that succeeded on its very last trial). When a bird graduated to an upper level but failed to eat on its first two trials there, it was brought

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back down to the previous level of difficulty (slightly modified from Carlier & Lefebvre, 1996). In this test, the dependent variable was the trial at which each bird reached each of the 4 levels of the learning task.

Two types of analysis were conducted on data from the three tests: first, the three groups of birds were compared via a multivariate analysis of variance to verify trends predicted from previous studies: if inter-group learning differences co-vary with differences in neophobia and tameness, we predict that gregarious pigeons should have lower mean latencies on all tests than group-feeding zenaida doves, who should in turn have lower mean latencies than territorial zenaida doves.

Our second type of analysis focuses not on between-group differences, but on individual performance: if neophobia and tameness are major determinants of learning, then individual variation in latency to learning should, in a multiple regression, be predictable from trials to eating in the neophobia and tameness tests. In order to tease out the relative effects of the individual, the species and the type of social organization, we also include in the regression model the latter two effects as dichotomous variables (species: pigeon vs dove; social: group-feeding vs territorial).

Results

All 61 birds ate within the limits of the tameness and neophobia tests. In the learning test, however, none of the zenaida doves reached level 4 of the task and very few reached level 3 (1 reached it at trial 39 in group StJ and 1 reached it at trial 31 in group DWH); conversely, all but 1 pigeon reached level 1 on trial 1 (1 reached it at trial 6). Trials-to-

criterion for the 4 levels in the 3 groups are illustrated in Figure 1. Since a single measure of learning is desirable for comparison with the two other tasks and since several groups yield little or no variance on 3 of the 4 levels, precluding statistical analysis, we used trials-to-criterion averaged for levels 1 and 2 as our index of performance on the hidden drawer task.

In the tameness test, presence vs absence of the experimenter had a strong effect on DWH doves, but practically no effect on either StJ doves or pigeons (Figure 2, Table 3). All pigeons ate on the very first presentation of food in day 4 (experimenter absent), precluding the use of these data in an Anova for lack of variance; inter-group differences in the presence vs absence of the experimenter will thus be statistically examined on days 1 to 3 only. A factorial analysis of variance (3 groups of birds x 3 repeated days) revealed significant main effects of the three columbid groups (F(2.58) = 11.162, p<0.001), as well as a significant main effect of the three test days (F(2, 116) = 16.472, p<0.001); the groups-by-days interaction was also significant (F(4, 116) = 5.452, p<0.001). Post-hoc comparisons among the three populations on the mean value of all three test days can be seen in Table 2: only pigeons differ significantly from StJ doves (F(2,58) = 3.673, p<0.05). Post hoc comparisons involving each of the tameness test days in the significant interaction (Table 3) showed that pigeons and StJ doves did not differ significantly from day 1 to day 3, unlike the group-feeding doves who differed significantly from day 1 to day 3 (F(2,58) = 3.990, p<0.05), and from day 2 to day 3 (F(2,58) = 5.773, p<0.01). We used day 2 as our measure of tameness for the rest of the analyses, since the experimenter is hidden in this trial as well as all those conducted on

neophobia and learning, and pigeons show no variance in the second test with experimenter absent, day 4.

Figure 3 illustrates the means and standard errors of the three tests: tameness (day 2), neophobia and individual learning (mean of levels 1 and 2). In all three tests, pigeons performed at a faster rate than the DWH doves, who in turn performed faster than the doves from StJ. The Manova yields significant effects for both the multivariate (F(6, 112) =16.723, p<0.01) and the univariate effects of the three tests (tameness: F(2, 58) = 11.398, p<0.001; neophobia: F(2, 58) = 14.966, p<0.001; learning: F(2, 58) = 52.773, p<0.001). Comparisons between means (Tukey, all at the 0.01 level) were run on all univariate F tests for the three populations. Results of these comparisons are summarized in Table 4; pigeons were significantly faster than both StJ and DWH doves in the neophobia and learning tests, while StJ doves were significantly slower than both pigeons and DWH doves in the tameness test (experimenter absent).

In the multiple regression (overall F(4,56)=52.681, p<0.001), both species (p<0.001) and neophobia (p<0.001) were significant predictors of learning performance; tameness and social organization were not (p respectively 0.624 and 0.859). We further decomposed the predictors of learning by running separate multiple regressions on pigeons and zenaida doves. In doves, neophobia (p<0.001) was again the only significant predictor of learning, with social organization (p = 0.894) again failing to reach significance (overall F(3, 35) = 9.611, p<0.001). When pigeons were analyzed alone, neither neophobia (p = 0.883) nor tameness (p = 0.281) significantly predicted individual variation in learning latency (overall, F(2, 19) = 0.837, p = 0.448). Under the assumption that our successive tests are like a markov chain and that the effect of tameness on learning is hidden within its effect on the neophobia test, we conducted another set of multiple regressions that excluded the learning test. For both pigeons and doves, performance in the neophobia test was significantly predicted by latency in the tameness test (pigeons: N = 22, F(1,20) = 11.792, p = 0.003; doves: N=39, F(2, 36) = 6.283, p = 0.005; social organization p = 0.792).

PART B: FIELD EXPERIMENT

Methods

Study Sites

For zenaida doves, field experiments were conducted on the island of Barbados during the months of May and June, 1997, in the same two areas as those used in the captive experiment, StJ and DWH. For pigeons, the experiments were conducted in Montréal, Québec from October to December, 1997. In each of the three areas (StJ, DWH and Montréal), field experiments were run at either of two randomly determined sites. At DWH and StJ (which are separated by 9km), the two sites were respectively 30 and 20 m apart. The StJ sites were on the grounds of Folkestone park and the nearby St-James Church; the two DWH sites were situated at the northern and southern ends of the Barbados Mills compound, out of view of one another. In Montréal, the sites were 3.83 km apart and situated in an urban park with heavy pedestrian traffic (Dominion Square) and a vacant car park near the Vendome metro station, in the more residential Notre-Dame-de-Grâce area.

Experimental Procedure

We used a procedure similar to the one described by Greenberg (1989). All three populations of birds were exposed to the same testing procedure: on every test day, birds were given a habituation trial by placing a patch of seed (20cm diameter) in the vicinity of individuals already present. A constant distance of 15 m was kept between the experimenter and the patch to enable the birds to feed, undisturbed, for a period of 10 minutes. During the habituation, a coin was flipped to determine whether or not a novel object was to be used in the following experiment. If a novel object was required, then the coinflipping procedure was repeated to select which of the following four objects was to be used: a red bowl, a black diving mask, a brightorange cracker box with inserted pine needles, and a square piece (40x40x8cm) of brown-coloured Styrofoam with smaller pyramidal shapes protruding at regular intervals from the surface. The objects were assumed to be unfamiliar to all three populations of birds.

Once the habituation period was over, the experimenter slowly approached the feeding area and placed a piece of twine around the patch of food (1.5 m diameter), in order to quantify and compare the number of birds in this area throughout all the trials; all birds sighted within the circle were counted during the trials. If required, the novel object was also placed within the circle next to the food patch. At a distance of 15 m from the food patch, the following data were scan sampled at 30 s intervals, for a duration of 20 min: (a) the number of pigeons (in Montréal) or zenaida doves (at StJ and DWH in Barbados) found within the circle, as well as (b) the number of individuals from any other avian species. In Montréal, these are likely to be house sparrows (Passer domesticus), European starlings (Sturnus vulgaris), and ring-billed gulls (Larus delawarensis); at DWH, they are likely to be feral pigeons (C. livia), carib grackles (Quiscalus lugabris) and glossy cowbirds (Molothurus bonariensis), while at StJ, they are likely to be carib grackles, lesser-antillean bullfinches (Loxigilla noctis) and common ground doves (Columbina passerina). Feeding latency per trial for the three

populations was derived from these observations and defined as the scan (in log seconds) where at least one pigeon (in Montréal) or zenaida dove (in Barbados) started to feed in the 1.5 m zone delimited by the twine. A second trial (also 20 min duration) was run immediately following the first trial, where the procedure for selecting a novel object was repeated, and the same observations were made at 30 s intervals. The experimenter always approached the food patch between trials (whether or not a novel stimulus was required) to replenish the food by the same amount present at the beginning of the first trial, and to remove and/or replace the novel object. In total, 20 sessions (habituation + 2 randomly determined trials) were conducted for each of the two zenaida dove populations and 19 for the feral pigeons.

Results

Consistent with previous studies, field experiments at DWH attracted a large number of zenaida doves, as well as a few carib grackles (mean = 0.59) and glossy cowbirds (mean = 4.70). At StJ, a single zenaida dove usually visited the experimental patch and defended it against conspecifics; carib grackles (mean = 0.92), bullfinches (mean = 0.22), glossy cowbirds (mean = 1.65) and ground doves (mean = 0.63) also fed at the patch with little or no aggression. In Montréal, large numbers of feral pigeons attended the patch in the habituation phase and no-object trials, with a few house sparrows (mean = 0.17), ring-billed gulls (mean = 0.08) and European starlings (mean = 0.05). Figure 4 shows that the presence of a novel object has a dramatically different effect on the three bird populations and that this effect is opposite to the one seen in the captive test of neophobia presented earlier. A 2x3 factorial Anova (data log transformed to normalize the variances) revealed a significant main effect of presence versus absence of a novel object near the food patch (F(1,112) = 47.129, p<0.001), and a significant main effect of type of bird (F(2,112) = 17.002, p<0.001). An Anova performed on the untransformed latencies to feeding yielded similar results.

Comparisons between means (Tukey tests, all at the 0.01 level) revealed significant differences between all three populations of birds in the presence of the novel object, as well as a significant difference in pigeons for presence versus absence of the novel object. Population means in the absence of the novel object are not significantly different. These effects are summarized in Table 5.

These trends are further illustrated in Figure 5, which plots the mean number of pigeons or zenaida doves per scan in the two conditions for the three populations of birds. In the absence of a novel object (Figure 5b), both the gregarious pigeons and group-feeding doves show a rapid increase in the number of individuals at the patch, followed by a progressive decline as the food is depleted; the number of StJ doves at the patch remains the mean value of 1 predicted by territorial foraging.

When a novel object is placed near the food patch, the curves for group-feeding and territorial doves show essentially the same pattern as they do in the absence of the novel object: a sharp rise followed by a slow decline for group-feeding doves, a stable curve value close to one bird per patch for territorial doves. In pigeons, however, the curve changes dramatically: very few birds fly down to feed in the presence of a novel object (Figure 5a), even in cases where a trial was prolonged to 40 minutes (not illustrated).

GENERAL DISCUSSION

Two main results stand out in this thesis: in Part a, the captive experiments established that feral pigeons performed faster than group-feeding zenaida doves on all tests, while group-feeding doves were in turn faster than territorial ones. In Part b, field experiments on neophobia showed a striking reversal of the trend seen in captivity: gregarious pigeons were the slowest of the three columbids at feeding next to an unfamiliar object, while territorial doves from StJ were the fastest. These two contrasting results have important implications for both the internal and external validity of comparative work.

Internal validity

In terms of internal validity, it seems clear that learning in columbids co-varies with at least two basic features of captive testing situations, the tendency to interact with a new stimulus (neophobia) and the latency to feed. As outlined in the Introduction, these two variables should be seen as intervening ones, whose theoretical role needs examining, rather than confounding ones, whose effect on learning needs to be eliminated. Tameness and neophobia may play a key role in behaviour modification in the field, influencing, for instance, the extent to which a species will adapt to new habitats, whether or not these are modified by human activity. No doubt due to the fact that comparative learning experiments originated in psychology, researchers have had a tendency to eliminate these co-variates a priori. In doing so, however, fundamental properties of learning variation may be masked. These properties may not only affect learning results in an experiment, but could have played a major role in the evolution of learning differences: when two species differ in a particular learning ability, it is possible that the difference is not a product of selection on the abilities per se, but on the tendency to rapidly look for food when hungry and explore new stimuli, thereby accelerating subsequent behaviour modification only as a side effect. Only further work on this issue can pinpoint whether it is learning itself or the stimulus and feeding precursors of learning that truly co-vary with ecological pressures.

Overall, the findings in part a of the thesis are consistent with results reported previously by Lefebvre et al. (1996) and Carlier & Lefebvre (1996). In separate two-way comparisons, both pigeons (Lefebvre et al., 1996) and group-feeding doves (Carlier & Lefebvre, 1996) learn faster than territorial doves. Lefebvre et al. (1996) further showed that pigeons fed faster than territorial doves in a familiar dish. My thesis, because it uses a three-way comparison, allows the two biological variables that were confounded in previous work, species and social organization, to be teased apart. Results suggest that species is probably a more important variable than social organization in explaining differences between the three columbids. A much larger proportion of the total variance is accounted for when pigeons are contrasted with the two zenaida dove populations than when the two group-feeding columbids are contrasted with the territorial one: species is significant in the anovas and manovas of Part a, while social organization is not. Furthermore, the learning difference between territorial and group feeding zenaida doves is so small compared to

the one that separates doves from pigeons that steps 3 and 4 of the learning task had to be kept out of statistical analyses (fig. 1).

This important effect of species is possibly caused by artificial selection on pigeons. All pigeons in the New World are feral descendants of domesticated stock brought from the Old World as food for European colonists; domestication may have involved intense artificial selection for tameness. Contrary to pigeons, zenaida doves in Barbados have never been domesticated, and have faced an evolutionary and cultural history that includes a low level of natural predation, save pressures from human hunting in the past few centuries (K. Watson, pers. com., UWI, Cave Hill, Barbados). This may explain why feral pigeons outperform zenaida doves on all three captive tests.

Alternatively, the results from the field may reflect varying degrees of sociality: pigeons not only undertake foraging, roosting and loafing in flocks, but they also take flight in a group as a social response to predators (Johnston & Janiga, 1995). When pigeons feed in groups, they often maintain no individual distance whatsoever, pratically walking on top of one another as they scramble for food. In constrast, zenaida doves are basically territorial, with a facultative option for group-feeding when food occurs in very large, temporally and spatially predictable patches that attract large numbers of competitors (Goldberg, 1998). Goldberg (1998) found that when the distribution of food was manipulated in space and time at the DWH, the normally group-feeding doves would start defending small, predictable clumps of food. Goldberg could not, however, get territorial doves from StJ to stop defending their territory when she gave them the same food distribution that leads to group-feeding at the DWH. Furthermore, group-feeding doves always maintain a minimum individual distance at DWH. They occasionally chase, and threaten each other even when group-feeding and do not, contrary to pigeons, respond as a flock to disturbances; each bird instead flies off alone (pers. observ.). There thus seems to be a gradient of gregariousness in the three columbids I tested: pigeons are true flockers that only use food defence in restricted conditions (Lefebvre & Henderson, 1986); at the other extreme are StJ doves, who are territorial year-round and do not stop defending even large, unpredictable patches (Goldberg, 1998). In between the two (but probably closer to StJ doves not only in terms of genetics, but also social foraging) are the temporarily aggregating DWH doves, who easily revert to defence as soon as food distribution favours it (Goldberg, 1998).

The multiple regression analyses on the captive learning data suggest that neophobia is a good predictor of individual learning, and that latency to feeding in the absence of a human, is in turn, a good predictor of neophobia. These results are confirmed and strengthened by a re-analysis of data previously obtained on grassfinches (Whittle, 1996). Using manovas, Whittle found that the similarity in his two species on the two social learning tasks he ran were no different from their similarity in a battery of four neophobia tasks and two individual learning ones. Whittle's use of eight tasks, however, could have introduced a large degree of relatively trivial variation in the results, potentially masking some important trends. If this is true, then combining the various neophobia, individual learning and social learning tasks into total scores could reveal interesting patterns. A re-analysis along these lines shows strikingly similar results to the ones obtained in

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my thesis: if we add individual trials-to-criterion for the 4 neophobia tests into a single neophobia score, then do the same for the two individual learning tasks (obtaining a single individual learning score for each bird) and the two social learning ones (data re-calculated from Whittle, 1996, given in Appendix A), a multiple regression similar to the one conducted in part a shows that individual learning score significantly predicts social learning score (p= 0.032) across the 40 birds Whittle tested, while neither species nor neophobia are significant (Appendix B). If we now do exactly what we did for columbids and take out the last learning score under the assumption that each successive effect is now the only significant predictor (p = 0.032) of individual learning score is now the only significant predictor (p = 0.032) of individual learning score for Whittle's 40 birds; species is again non-significant. (Appendix B). Figure 6 summarizes in a flow chart the effects of these successsive predictors in both finches and columbids.

External validity

The finding that learning differences between group-feeding and territorial columbids co-vary with intervening traits does not really pose a theoretical or methodological challenge to comparative work on this group. As sugested above, all that needs to be done is to incoporate the intervening variables into the ecological program and further test for the relative role of the different variables in adaptive diferences between species or populations. However, the finding in part b that captive and field tests of neophobia can produce opposite results is more disturbing. In Greenberg's (1989, 1990) experiments, the more generalist opportunist *Melospiza* species was also less neophobic in both captive <u>and</u> field experiments. This provides key experimental evidence of the ecological validity of the captive test.

In the case of columbids, the result is very different. In the field, a group-feeding bird appears to use others as a source of information about novel objects. In the case of group-feeding doves, similar numbers of birds eventually come down to feed next to the novel object, but recruitment is slower, as seen in the rate of increase of the curve illustrated in Figure 5a. For pigeons, this inhibitory effect extends to the number of birds actually coming down to feed: large numbers of pigeons remain perched near the food source when a novel object is placed close to it, but do not fly down to feed .

This inhibitory effect of the group does not seem to occur in single birds: a caged, single pigeon and a caged, single zenaida dove feed in a novel feeding apparatus with the same relative latency (i.e. pigeons faster than doves) they show in learning and in simple feeding from a familiar dish. As would be predicted from this single vs group effect, territorial doves essentially show the same latency to feed whether a novel object is placed or not near to the food.

Overall, these results suggest that social organization is not an easy variable to use in comparative learning experiments. By definition, these experiments have to be conducted on caged single subjects, lest the apparent effect of the contingencies being investigated be due to the effects of other individuals or stimuli. Part A of this thesis shows that within the confines of this single cage procedure, the response of the different types of birds is internally consistent across all tests, and therefore internally valid. Whether the tests are externally valid is another matter. If the goal of a captive learning test on a group-feeding vs a territorial bird is to assess its natural capacity to respond to new situations, then the captive test is inappropriate. This further adds to the problems that plague comparative studies whose ecological correlate is social organization. Since social organization is so flexible and often adjusts very rapidly to economic conditions in the field (Brown, 1964; see also Goldberg, 1998 for a review), animals may have very flexible learning rules to deal with the effects of competitor pressure. Differences between group-living and territorial animals are consequently likely to be learned rather than fixed by natural selection, contrary to learning rules that seem to apply to filial imprinting, spatial memory and song imitation. Predictions from adaptive specialisation and general process theories cannot be distinguished when the learning difference predicted from ecology is itself learned. This thesis therefore adds a further caveat to comparative studies focusing on social organization.

Conclusion

In conclusion, the ability to predict social learning from individual learning differences, which can also be predicted from neophobia, has far-reaching consequences for future studies of learning. Psychologists need to consider the implications of wiping out differences in intervening variables through pre-experimental handling and habituation; as this may remove a key variable that is part of the complex of traits selected to help animals respond rapidly to new situations. This also makes interspecific or interpopulation differences uninterpretable,

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because many key differences have been erased before the experiment. Future studies should remain focused on the effects of social foraging on learning, but researchers should realize that these effects are very general. This study found that a complex of related traits (that includes tameness and neophobia as well as individual and social learning) may favour a rapid response to new situations. In a groupliving animal, this set of responses may be internally consistent in the isolated conditions of captive testing, but may have little external validity and differ sharply from social responses to novelty in the wild. If this is the case, one should seriously question the future of comparative learning experiments with social variables.

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FIGURES

Figure 1. Differences between the 3 populations of columbids on mean trials-to-criterion for the 4 task levels of the individual learning test







Figure 3. Mean latency to feeding in three captive experiments for three populations of columbids.



Figure 4. Mean feeding latency in the field for the three bird populations with or without a novel stimulus.



Figure 5a. Mean number of birds per scan in the presence of a novel object in the three populations of birds.



Figure 5b. Mean number of birds per scan in the absence of a novel object in the three populations of birds.



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Figure 6. A Flow Chart Illustrating the Role of Intervening Variables on Individual and Social Learning.



Pigeon > Group-Feeding Dove > Territorial Dove

(this thesis)

TABLES

Table 1. Operational definitions of the 4 task levels (modified from Carlier & Lefebvre, 1996).

Level of difficulty	Position of drawer	Seed accessibility	Behaviour sufficient for eating seed
Level l	Half open, half under drawer roof	Half directly accessible	Peck sideways under drawer
Level 2	Open to edge of well, well visible	Not accessible unless drawer pecked or pulled	Insert beak at edge of well and pull
Level 3	Open to 5mm of edge of well	Fully hidden	Pull at drawer edge
Level 4	Fully closed	Fully hidden	Pull ring
Table 2. Post-hoc comparisons between the mean value of latency to feeding for the sum of all three tameness tests on the three populations of columbids.

	Pigeons	DWH	StJ
Pigeons		2.596	3.673
		ns	p<0.05
DWH			1.077
			ns

(ns = non-significant)

Table 3. Post-hoc comparisons between population means (Tukey tests) of the 3 tameness tests run in the presence and absence of the experimenter.

	1									
		Pigeon			DWH			StJ		
		Present	Absent	Present	Present	Absent	Present	Present	Absent	Present
		Day 1	Day 2	Day 3	Day 1	Day 2	Day 3	Day 1	Day 2	Day 3
Pigeon	Present Day 1		2.992	3.174						
			ns	ns						
	Absent Day 2			0.182						
				ns						
DWH	Present Day 1					3.270	3.990			
						ns	p<0.05			
	Absent Day 2						5.773			
							p<0.01			
StJ	Present Day 1								1.097	0.299
									ns	ns
	Absent Day 2									0.997
										ns

(ns = non-significant)

Table 4. Variables that significantly affect group differences in acaptive learning experiment.

	Pigeons	DWH	StJ
Pigeons		Neophobia	Tameness
		Learning	Neophobia
			Learning
DWH			Tameness

Table 5. Comparisons between mean feeding latency (Tukey tests, all at the 0.01 level) for the three columbid populations in the presence and absence of a novel object.

		Pigeons		DWH		StJ	
		Novel	Normal	Novel	Normal	Novel	Normal
Pigeons	Novel		12.18, p<0.01	6.13, p<0.01		11.27, p<0.01	
_	Normal				2.21, ns		<1.00, ns
DWH	Novel				3.84, ns	5.14, p<0.01	
	Normal						2.12, ns
StJ	Novel						<1.00, ns
	Normal						

(ns = non-significant)

APPENDIX

(A) Raw data used in the re-analysis of Whittle's (1996) data on grass finches.

SPECIES	NEOPHOBLA	INDIVIDUAL	SOCIAL LEARNING
		LEARNING	
Amadina fasciata			
	6.250	35.000	67.000
	8.750	39.500	65.000
	8.750	24.500	37.500
	12.250	34.000	48.000
	2.750	33.000	37.500
	11.250	28.000	40.000
	8.500	23.500	50.500
	11.000	44.000	30.000
	5.500	31.500	
	3.000	15.500	
	5.750	17.000	12.500
	3.500	25.000	49.500
	11.750	49.000	43.000
	7.250	39.000	33.500
	7.000	45.500	44.000
	6.750	32.000	7.000
	7.750	29.500	43.000
	1.250	31.500	29.500
	15.000	38.000	35.000
Taanamusia autota	2.300	24.000	17.300
Taenopygia gullala	12 000	18 000	<u>60 000</u>
	8 000	+0.000 37 500	26,000
	13 250	25,000	50.000
	10,500	23.000	12,000
	8 750	43 500	70,500
	10 500	37 500	13 000
	6 750	30,500	43.000
	7.000	25 500	
	6,750	40,500	
	3.000	20.000	
	5.750	40.500	59 500
	7.250	41.000	62,500
	6.000	40.000	45.000
	6.750	44.000	54.500
	3.500	23.000	17.500
	5.000	28.000	42.000
	2.250	44.500	15.500
	5.000	44.500	56.500
	13.250	37.500	51.500
	7.250	29.500	38.500

(B) Results from the re-analysis of Whittle's (1996) results using the multiple regression approach

Dependent variable: Social learning	
Independent variables:	'p'
1. Species	0.369 , ns
2. Neophobia	0.077, ns
3. Individual learning	0.032
Multiple regression: $F(2, 31) = 5.354$, p=0.010, r ² = 0.209	
Dependent variable: Individual learning	
Independent variables:	
1. Species	0.133, ns
2. Neophobia	0.032
Multiple regression: $F(2, 37) = 3.572$, $p=0.038$, $r^2 = 0.117$	