



*Cover drawing by Sue Anne Zollinger*

“...the straightforward application of Darwinism to cognition seems a better idea day by day. Evolutionary convergence and divergence are two sides of the same biological picture, and any call for moving apart from one or the other is surely ill advised. In the case of tool use, the straightforward application of Darwinism implies enriching our knowledge of cognitive differences between close relatives, and relating this to the known ecology of the species in question.”

---

– Alex Kacelnik

(2009) Tools for thought and thoughts for tools. *Proceedings of the National Academy of Sciences of the USA*. 106: 25, p 10072



## PREFACE

---

This thesis was written during the time I spent at the Max Planck Institute for Ornithology in Seewiesen from October 2007 to February 2011. I was hosted at the Department of Behavioural Ecology and Evolutionary Genetics of Bart Kempenaers and for the last few months at the Sensory Ecology Research Group of Björn Siemers. However, my main thesis supervision was done by Sabine Tebbich of the Department of Cognitive Biology at the University of Vienna.

This work grew out of two field seasons which I spent in the Galápagos in 2007 and 2008. My project was funded by the DFG (Deutsche Forschungsgemeinschaft, Germany) for the first two years of my doctoral studies and then from Sabine Tebbich's FWF grant (Förderung der wissenschaftlichen Forschung, Austria) for the last year.

My thesis addresses the factors driving cognition in Darwin's finches with a special focus on tool-use in the woodpecker finch (*Cactospiza pallida*). Chapter 4 was published in April 2010 in a special issue of the *Philosophical Transactions of the Royal Society B* on Darwin's finches. Chapter 2 was accepted by *Animal Cognition* shortly before I submitted this thesis and Chapter 1 has been submitted to *Animal Behaviour*.



# TABLE OF CONTENTS

---

LIST OF FIGURES AND TABLES .....	<i>page ix</i>
GENERAL INTRODUCTION .....	<i>page 1</i>
CHAPTER 1      Sometimes Tool-use is Not the Key: No Evidence for Cognitive Adaptive Specializations in Tool-using Woodpecker Finches .....	<i>page 17</i>
CHAPTER 2      Physical Cognition and Tool-use: Performance of Darwin's Finches in the Two-Trap Tube Task .....	<i>page 35</i>
CHAPTER 3      Investigating the relationship between extractive foraging and learning abilities in two species of Darwin's Finches .....	<i>page 49</i>
CHAPTER 4      The Tale of the finch: adaptive radiation and behavioural flexibility .....	<i>page 73</i>
GENERAL DISCUSSION .....	<i>page 91</i>
SUMMARY .....	<i>page 99</i>
ZUSAMMENFASSUNG .....	<i>page 101</i>
ACKNOWLEDGEMENTS .....	<i>page 103</i>
REFERENCES .....	<i>page 105</i>
APPENDICES:	
APPENDIX 1      History of experimental subjects .....	<i>page 115</i>
APPENDIX 2      Details of methodology and statistical procedures of Chapter 1 .....	<i>page 117</i>
APPENDIX 3      Data and detailed statistical results of Chapter 1 ....	<i>page 123</i>
APPENDIX 4      Testing conditions, experiment order and time elapsed between Experiments 1-2 of Chapter 2 .....	<i>page 128</i>
APPENDIX 5      Counterbalanced design of the LNR and P reversal conditions of Chapter 3 .....	<i>page 131</i>

APPENDIX 6	Supplementary movies of subjects performing in Experiments 2-3 of Chapter 1 .....	<i>see enclosed CD-rom</i>
LIST OF PUBLICATIONS .....		<i>page 132</i>
AUTHOR'S CONTRIBUTIONS/ ABGRENZUNG DER EIGENLEISTUNG .....		<i>page 133</i>
ADDRESSES OF CO-AUTHORS .....		<i>page 134</i>
ERKLÄRUNG DER SELBSTÄNDIGEN ANFERTIGUNG .....		<i>page 135</i>

*A CD-ROM containing supplementary Movies (Appendix 6) is enclosed along with the thesis.*

Please note that Chapter 4 has already been published. Therefore, in my thesis this chapter is generally cross-referenced as “Tebbich et al. 2010” whereas all other chapters reference by chapter number. For example, to reference my published chapter, I would write “see Tebbich et al. 2010” whereas for Chapter 1 (unpublished), I would write “see Chapter 1”.

Chapter 4 is included in its published form with some minor formatting modifications so that it fits the style of this thesis. Furthermore, Figures 1.1. and 1.2 were originally published in Tebbich et al. 2010, but to avoid repetition and to keep the flow of the thesis these figures appear in Chapter 1 and are not included again in Chapter 4.

# FIGURES AND TABLES

---

## GENERAL INTRODUCTION

**unnumbered Figure** Woodpecker finch using a tool to probe into a substrate ..... *page 12*

## CHAPTER 1

**Figure 1.1** Theseesaw apparatus..... *page 22*

**Figure 1.2** The cane task apparatus ..... *page 23*

**Figure 1.3** The box opening task apparatus ..... *page 24*

**Figure 1.4** Logistic regression models of success probability across trial number for two-choice learning tasks (reversal learning, seesaw and cane tasks) ..... *page 28*

**Figure 1.5** Cane task transfer performance ..... *page 30*

**Table 1.1** Test statistics comparing perseverance by group for the initial phases of the seesaw and cane tasks and both phases of the reversal task..... *page 29*

**Table 1.2** Descriptive statistics quantifying perseverance by group for the initial phases of the seesaw and cane tasks and both phases of the reversal task ..... *page 30*

## CHAPTER 2

**Figure 2.1** Schematic illustrations of two-trap tube apparatus ..... *page 41*

**Figure 2.2** Performance of all birds in the initial phase of the modified two-trap tube with pre-inserted stick ..... *page 43*

**Figure 2.3** Performance of all birds in the initial phase of the modified two-trap tube without pre-inserted stick ..... *page 46*

## CHAPTER 3

**Figure 3.1** Schematic illustration of the perseverance (P) and learned non-reward (LNR) reversal concepts ..... *page 67*

**Figure 3.2** Objects used in measuring novelty reactions ..... *page 68*

**Figure 3.3** Between-species comparison of LNR and P reversal learning performance ..... *page 62*

**Figure 3.4** Within-species comparison of LNR and P reversal learning performance ..... *page 63*

**Figure 3.5** Comparison of learning performance in the first and second acquisition learning phase experienced by species .....page 64

**Figure 3.6** Comparison of neophobia to a control feeding latency for woodpecker finches and small tree finches .....page 65

**Figure 3.7** Consistency of neophobic responses .....page 66

**Table 3.1** Spearman’s correlations between (a) neophobia and reversal learning and (b) neophilia and reversal learning in the three reversal conditions..... page 67

**Table 3.2** Relationship between the number of positive reinforcements in the acquisition phase of each of the three reversal conditions and neophobia .....page 68

CHAPTER 4

**Table 4.1** Comparison of reversal performance between pigeons, three corvid species and three species of Darwin’s finches ..... page 100

APPENDICES

**Table A1** Subject’s experiment participation and history .....page 115

**Table A3.1** Raw data used in the assessment of the effect of apparatus malfunction occurrences on success in the seesaw task for each bird .....page 123

**Table A3.2** Generalized linear mixed model (binomial error) showing the effect of group, trial number and condition on success probability for the Seesaw and cane tasks. ....page 124

**Table A3.3** Generalized linear mixed model (binomial error) results showing the effect of group and trial number on success probability for both phases of the reversal task.....page 124

**Table A3.4** Post hoc tests for cane, seesaw and reversal task models .....page 125

**Table A3.5** Summary statistics of point of steepest slope by group for the cane and seesaw tasks and both phases of the reversal task .....page 125

**Table A3.6** Summary statistics of percent errors by group for the cane and seesaw tasks and both phases of the reversal task .....page 125

**Table A3.7** Statistical results of the comparison of point of steepest slope for the cane and seesaw task and both phases of the reversal task by group ..... page 126

**Table A3.8** Statistical results of the comparison of percent errors for the cane and seesaw task and both phases of the reversal task by group ..... page 126

**Table A4** Details of testing conditions, experiment order and time elapsed between Experiments 1-2 (Chapter 2) .....page 128

**Table A5** Counterbalanced design of P and LNR conditions (Chapter 3) showing the rewarded (+) and non-rewarded (-) colour stimuli for each acquisition and reversal phase .....*page 131*



## GENERAL INTRODUCTION

---

We see animals doing a multitude of different things in the world. Some of these behaviours seem so intelligent and human-like, that we can't help asking what cognitive abilities lie at the bottom of such a display. Do they think like us and do they see the world as we do? From our anthropocentric viewpoint, it is sometimes hard to imagine otherwise. Clearly some animal behaviours seem more surprising and interesting to us than others, generally those that we associate with the human lineage including tool-use, social intelligence, solving novel problems and planning for the future to name just a few examples.

The questions we generally ask ourselves when witnessing uncannily human-like animal behaviour is “what are the limits of this animal's cognitive complexity and how does it compare to our own intelligence?”

Tool-use is a prime example of a remarkable human-like behaviour that is also found in other animals. Technology was once thought to be the sole domain of humans and a key aspect of our identity as a species. As late as 1949, the anthropologist Kenneth P. Oakley (1949 p. 1) wrote in his work *Man the Tool-Maker* “employment of tools appears to be [man's] chief biological characteristic”. Tool-use in humans is marked by a conceptual grasp of physics and generally involves planning and mental representation to achieve a goal. Thus, it is no surprise that the discovery of animal tool-use captivated the scientific world. The resemblance of animal tool-use to our own behaviour forced us to acknowledge the possibility that we are not alone, that the origin of our own intelligence might be found in our close and perhaps even in our distant animal relatives.

While many definitions of tool-use have been proposed, the working definition that I will use throughout this thesis is that of Beck (1980 p. 10) who defined tool-use as:

“the external employment of an unattached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the

user itself when the user holds or carries the tool during or just prior to use and is responsible for the proper and effective orientation of the tool”.

Regardless of which definition is used, a degree of subjectivity and ambiguity always remains. Nevertheless, the examples of tool-use which I give in the following can all be considered tool-use according to Beck's widely used definition, unless otherwise specified.

## EXAMPLES OF ANIMAL TOOL-USE

Nearly 5 decades have passed since Jane Goodall published the first observations of non-human animals using tools in a manner reminiscent of human tool-use: she reported her observations of chimpanzees (*Pan troglodytes*) which had fashioned tree stems for use in extracting termites from their mounds (Goodall 1964). Since then, there has been an explosion of reports of animal tool-use originating from seven classes of animals: Insecta, Malacostraca, Gastropoda, Cephalopoda, Actinopterygii, Aves and Mammalia (Bentley-Condit and Smith 2009).

Chimpanzee tool-use has proven to be most wide-ranging of all non-human animal tool-users: they use a wide variety of tools including stones to crack open hard nuts and ‘tool kits’ with different functions that are employed in the extraction of different food types. Not only do they employ a diversity of tools, but their tools are also used in a wide range of contexts from food-gathering to social contexts and self-maintenance and there is cultural variation in tool-use between different populations (see McGrew 2010 for a review of chimpanzee tool technology). Some populations of orang-utans (*Pongo pygmaeus*) also use tools regularly in the wild (reviewed in van Schaik et al. 2003) while the remaining great apes only rarely show tool-use in their natural settings [e.g. gorillas (*Gorilla gorilla*): Breuer et al. 2005; bonobos (*Pan paniscus*): reviewed in Gruber et al. 2010]. Nevertheless, laboratory studies suggest that even these non-habitual tool-using great apes possess considerable latent tool-using abilities (e.g. Herrmann et al. 2008; Lonsdorf et al. 2009; Manrique et al. 2010; Pouydebat et al. 2005). Amongst non-human primates, capuchin monkeys (*Cebus sp.*) are particularly well-known for their stone tool-use (reviewed in Ottoni and Izar 2008).

Outside the realm of primates, we find many other examples of mammal tool-use, including african and asian elephants (*Loxodonta africana* and *Elephas maximus*) that use switches to free themselves from parasites or objects to repel an adversary in an antagonistic interaction (e.g. Chevalier-Skolnikoff and Liska 1993; Hart and Hart 1994), beavers (*Castor fiber*) that likewise use objects in antagonistic displays (Thomsen et al. 2007) and bottlenosed dolphins (*Tursiops truncatus*) that wear sponges over their rostrum apparently to probe into substrate while foraging (Krützen et al. 2005; Mann et al. 2008; Smolker et al. 1997).

Some even more unlikely tool-users include hermit crabs (*Dardanus sp.*) that use anenomes to ward off predators (Ross 1971), ant lion larva (*Myrmeleon sp.*) that flick sand at prey near the edge of its trap thus causing them to fall in (Wheeler 1930), and digger wasps

(*Sphex sp.*) that use a pebble held in the mandible as a hammer to pound dirt, thereby sealing the entrance to their nest burrow (Peckham and Peckham 1898).

Habitual tool-use in the wild has also evolved in several bird species. For example, Egyptian vultures (*Neophron percnopterus*) drop stones on ostrich eggs (van Lawick-Goodall and van Lawick 1966), green-backed herons (*Butorides striatus*) use bait to catch fish (Walsh et al. 1985), satin bower birds (*Ptilonorhynchus violaceus*) use bark-wads to paint their bower (Chaffer 1945), and woodpecker finches (*Cactospiza pallida*) use twigs or cactus spines to retrieve insects and spiders from tree holes (Eibl-Eibesfeldt 1961). Certainly the most diverse and complex avian tool-use known is that of New Caledonian crows (*Corvus moneduloides*): these birds make and use at least three forms of tools to aid prey capture (Hunt 1996; Hunt and Gray 2002, 2004a, b).

The long list of behaviours that have been classified as animal tool-use shows that there is great variation in animal tool-use ranging from species that use found objects as tools in a stereotyped way and only in a specific set of circumstances to those that manufacture their own tools, carry them long distances before using them and use a great variety of tools in many different contexts. Therefore, it would be much too simplistic to presume that animal tool-use *per se* is associated with cognitive complexity and indeed this is widely recognized (e.g. Alcock 1972; Beck 1980, 1986; Bluff et al. 2007; Emery and Clayton 2009; Hall 1963; Hansell 1987; Tebbich et al. 2010).

Some types of animal tool-use are thought to signify more complex information processing abilities than others. The filter used to pinpoint tool-use suggestive of cognitive sophistication varies in its components. Kacelnik et al. (2006) concisely summarized some of the key characteristics to be taken into account in such a diagnosis. They place weight on the diversity of tool types and materials used, on whether tools are manufactured (with further differentiation based on the complexity of manufacture), on the frequency of tool-use in the species, and on population differences in tool-use that are suggestive of cultural transmission. It is furthermore worthwhile to take note of the point made by Bluff et al. (2007, p. 2) that the “motor complexity of a behaviour offers no guide to its underlying cognitive complexity”.

## **THE CORE QUESTIONS: FROM AN ANTHROPOCENTRIC TO AN ECOLOGICAL APPROACH**

Of all the examples of animal tool-use, it is mainly the complex forms of tool-use such as those documented in primates and recently also in New Caledonian crows, that have driven the core questions of animal tool-use research. Probably due to the historically rooted perception of tool-use as a hallmark of human intelligence and the subsequent stir created by the discovery of animal tool-use, research in this field has long been dominated by the anthropocentric approach. The main question fuelling this research has been classically *scala naturae*, that is are the cognitive abilities of humans and animals on a continuum or do one or several

qualitative delimiting differences exist between humans and animals?

However another anthropocentrically driven evolutionary question became popular later and subsequently stimulated many studies on animal tool-use, namely, the question of whether tool-use acted as a driver of human intelligence or whether it is merely the expression of general intelligence that evolved in another context (e.g. Byrne 1995). It might be helpful to flesh out the hypothetical scenario in which tool-use could have driven human intelligence. The idea is that as tools gained importance in the lives and survival of early hominids, selection acted upon the heritable (cognitive) traits of these early humans that improved their tool-related competence (e.g. Parker and Gibson 1979). This evolutionary scenario can also be applied to non-human tool-users and the hypothesis that tool-use acted as a driver of cognitive abilities can be tested with a comparative approach.

If tool-use is an evolutionary driver of intelligence we would expect to find convergent cognitive abilities in tool-using animals and divergence in closely related tool-using and non-tool-using animals. However, since for a long time this question was inspired by a desire to understand humans and not the animals themselves, the ecology of tool-using animals has been largely ignored. The effect was a channelling of the field of comparative cognition so that focus was primarily on certain behaviours (the human-like ones), in certain animals (mostly in primates and within primates, specifically on apes because of their close relation to humans), and on certain questions (mostly proximate questions regarding cognitive mechanisms and evolutionary questions informing the evolution of human intelligence). Such an anthropocentric approach can never lead to a complete understanding of the animal behaviours that they seek to “explain” (explain in terms of humanness).

Happily, the past few decades have witnessed a shift in the focus of comparative cognition studies, particularly amongst non-primatologists, towards a much more animal-centered and ecological approach in attempts to understand animal cognition. This approach focuses on the adaptive value of cognition, that is, it emphasizes information processing as an adaptation to solve ecological challenges and the evolution of cognition for each species, rather trying to understand cognition in light of human intelligence (Balda and Kamil 1989; Shettleworth 1993, 1998).

## **Cognitive adaptive specialization hypothesis**

One of the most important ideas of the ecological approach, is the adaptive specialization hypothesis (Rozin and Kalat 1971). This hypothesis states that, similar to morphological adaptive specializations of bird beaks to different food types, we should expect the evolution of adaptive specializations in information processing for different cognitive challenges posed by an animal's environment. The hypothesis predicts that brain areas and specialized learning skills that are most vital in dealing with the given environmental challenge should be more highly developed than in other close relatives which do not face this challenge. A classical example of the link between learning specialization and life history are rats

which are generalist feeders and have the capacity to acquire first-trial flavor aversions even with delays of hours between ingesting something with a certain flavor and the onset of its effects (Garcia et al. 1966). More recently, this integrative approach has been applied successfully and rigorously to the issue of scatter hoarding in animals. Scatter hoarding refers to the hiding of various items (usually food) in different places, which are widely distributed across their home range (Smulders et al. 2010). Intense research over the last three decades that demonstrated an exciting link between scatter hoarding animals, namely an enhanced processing of spatial information and hippocampus size (reviewed in Healy et al. 2009; Healy et al. 2005; Shettleworth 2003; Smulders et al. 2010; but see also criticism by Bolhuis and MacPhail 2001).

## How the adaptive value of tool-use could hone cognition

Tool-use in foraging is an innovative behaviour<sup>1</sup> that in most cases is likely to be an adaptation evolved in response to environmental challenges. If tool-use is adaptive and if it poses a cognitive challenge, then we would expect that enhanced cognitive abilities would have evolved to increase the effectiveness of tool-use or the efficiency of its ontogenetical development. Such enhanced cognition might also have enabled the evolution or ontogenetic development of such an unusual technique in the first place. A detailed knowledge of the ecology of a tool-using species and the characteristics of its specific tool-use can provide clues that help to formulate predictions about which specific aspects of cognition should be enhanced in each tool-using species (Smulders et al. 2010).

Neurobiological findings provide evidence in support of the notion that tool-use in some animals is cognitively challenging. For example, tool-use (*sensu* Beck) is strongly correlated to brain size in birds (Lefebvre et al. 2002) and primates (Reader and Laland 2002), the cerebellum of tool-using birds has a higher degree of folding than that of non-tool-using birds (Iwaniuk et al. 2009) and the associative brain areas of New Caledonian crows, a tool-using corvid species, are significantly larger than three other passerine species including other corvids (Mehlhorn et al. 2010).

---

<sup>1</sup> I use Kummer and Goodall's (1985, p. 205) definition of innovation throughout this thesis: "innovation can be: a solution to a novel problem, or a novel solution to an old one". This includes the discovery of a new resource such as a novel food item, the application of an established behaviour to a novel purpose or the invention of a completely novel behaviour.

## METHODS AND ISSUES IN THE INVESTIGATION OF TOOL-RELATED COGNITION

### Physical cognition and tool-use

What sort of cognitive enhancements should be expected to be linked to tool-use? One widely proposed enhancement has been that of “physical cognition”. Physical cognition refers to an ability to learn abstract and widely applicable rules about the physical interactions of objects in the environment. Sensitivity to the principles underlying functional tool-use could be an adaptive advantage because it could extend the selectivity, flexibility and innovativeness of this behaviour (Seed and Byrne 2010). The alternative to using a “high-level” generalized mechanism rooted in physical cognition, is “low-level” associative- or trial-and-error learning. Simple mechanisms have their own advantages. First and foremost, they might be easier and quicker to acquire in ontogeny [woodpecker finches developed fully functional tool-use less than 60 days after fledging (Tebich et al. 2001) while young chimpanzees in west Africa learn to use tools between the age of 3-5 years of age if ever (Inoue-Nakamura and Matsuzawa 1997)] and where the requirements of tool-using problems are stable, a simple rule would be widely applicable and of similar efficiency as tool-use with sophisticated underlying cognition.

### Tool-related cognition in primates and birds

Identifying the cognitive mechanisms underlying animal tool-use has been one of the main goals in the field of animal tool-use research and a large body of literature on the subject is now available. Investigations in this field have mainly been conducted with primates and have focused on the complex cognitive mechanisms that are thought to be related to the flexibility and efficiency of tool-use seen in some species, though in the last decade the field has expanded somewhat to incorporate more study organisms and new questions. In the following, I will summarize the most important findings concerning the underlying psychological mechanisms and ontogeny of animal tool-use.

Animal tool-use studies have been concerned in particular with the characterization of animal's understanding of the physical interactions governing tool-use (physical cognition, see above) and within this field there has been a special interest in causal reasoning, understanding of functional tool properties, and the ability to form novel solutions to novel problems. Another main area of interest has been the planning and goal-directedness involved in tool-use.

Great apes and capuchin monkeys (*Cebus sp.*) have been the subject of the bulk of studies on tool-related cognition (reviewed in Emery and Clayton 2009; Ottoni and Izar 2008; Seed and Byrne 2010; Visalberghi and Tomasello 1998) though a small number studies have also investigated the tool-related cognitive abilities of non-tool-using primates (e.g. lemurs

(*Eulemur fulvus* and *Lemur catta*): Santos et al. 2005a; cotton-top tamarins (*Saguinus oedipus*): Hauser 1997; Hauser et al. 2002a, b; Spaulding and Hauser 2005; Santos et al. 2005b; Santos et al. 2006; marmosets (*Callithrix jacchus*): Spaulding and Hauser 2005; vervet monkeys (*Cercopithecus aethiops*): Santos et al. 2006). Despite the large number of studies utilizing a variety of clever paradigms, there is still no unequivocal evidence that chimpanzees or other great apes possess information processing abilities similar to humans regarding the physical regularities governing tool-use (e.g. Penn et al. 2008; Povinelli 2000).

More recently there has been great enthusiasm for the tool-related cognition of New Caledonian crows, the only corvid species known to habitually use tools in the wild. In the wild, these crows use a variety of different tools and display population-level variation in their tool-use that is suggestive of cultural transmission of tool-use manufacturing methods (reviewed in Bluff et al. 2007). In the laboratory, these crows appropriately select and modify tools for a given task (Chappell and Kacelnik 2002, 2004) and they display elements of planning as demonstrated by their remarkable performance in meta-tool tasks that require subjects to use tools to gain access to other tools which can in turn be used to reach a food reward (Taylor et al. 2007; Wimpenny et al. 2009). Finally, one New Caledonian crow, “Betty”, famously created a new functional tool spontaneously from a novel material to solve a problem (Weir et al. 2002). To date, the performance of New Caledonian crows in various tasks testing physical cognition, indicates that their appreciation of these problems lies somewhere between a high-level understanding of the physical principles and low-level appreciation based on associative learning (Bluff et al. 2007; Emery and Clayton 2009).

Despite the remarkable tool-related cognition of New Caledonian crows, tool-use in this species emerges in ontogeny without social input (but see also Kenward et al. 2006; Kenward et al. 2005). This stands in contrast to chimpanzees who require years of observation to learn nut-cracking and termite-fishing techniques (Biro et al. 2003; Lonsdorf 2006).

## **Low- and high-level mechanisms: oversimplification of the problem**

At this point, I feel that it is warranted to give some background regarding one of the most contentious issues in studies of animal cognition. The problem is how to differentiate between low- and high-level cognitive mechanisms—the famed quest for intelligence—in non-verbal animals. Confronted with a human, we can simply ask questions to assess the level of understanding and cognition involved in a given task. In non-verbal animals, the assignment of the label “complex cognition”, “sophisticated cognitive strategy” or any other euphemisms for “intelligent” to a behaviour generally requires a demonstration that it is not the outcome of simple associative processes, the so-called “killjoy” explanations of animal cognition (Shettleworth 2010). Therefore, intelligence in animals is usually defined by exclusion rather than by the actual mechanisms involved (Seed et al. 2009). Examples of some high-level cognitive mechanisms that have been proposed are reasoning, logical inference,

and understanding (Bluff et al. 2007). There is a bewildering number of supposed mental processes that cannot be boiled down to simple associative processes—they have in common that they are notoriously difficult to pin down (e.g. Byrne and Bates 2006). A further aspect common to most attempts to pinpoint intelligence is high degree flexibility and adaptiveness to new situations.

Heyes (1993) suggested a method that has been widely adopted in laboratory studies by comparative psychologists for differentiation between low- and high-level cognitive mechanisms in problem-solving. Her “triangulation” method involves repeatedly exposing subjects to a problem until they have learned to solve it. To differentiate between high-level and low-level cognitive solutions, in following “transfer” presentations, the perceptual features of the task are varied while the underlying principle governing the task remains the same. Emphasis in the transfer tasks is on immediate success in order to exclude the possibility of a solution through fast perceptual learning. The idea is that an animal that had formed a rule based on a general principle will be able to cope with perceptual variations in the presentation of the problem as long as the underlying principle remains the same whereas the use of simple perceptual features to solve the task is effective in a very specific situation but should fall apart once the problem-features vary.

Heyes’ approach is useful, however it also contains some pitfalls. One is that it is impossible to control for all arbitrary cues that may be used in solving a task (Visalberghi and Tomasello 1998). Another problem is posed by the increasing evidence that even humans often make decisions in everyday life using simple heuristics rather than reasoning (e.g. Seed and Byrne 2010; Shettleworth 2010; Silva et al. 2005). In the case of humans, we know that they are capable of reasoning even if they don’t always use this ability because we can ask. Unfortunately, with animals, our questions are limited to clever tests, the outcomes of which often leave ample space for speculation.

Is it necessary or even useful to distinguish between high- and low-level strategies? I agree with Chappell (2006, p. R245), who summed up the situation aptly when she wrote:

“There has been a tendency to try to fit animals’ cognitive abilities into one of two categories: either they exhibit abilities equivalent (or nearly so) to those of humans, or their abilities are based on associative learning, and are therefore somewhat inflexibly tied to the specific stimuli used during training. The real situation is likely to be much more complicated than this, and the details of what is and what is not understood, and how those differ between species and between tasks are fascinating.”

“The details of what is and what is not understood” hints at what is perhaps currently the single greatest problem in comparative psychology, namely the construction of a “cognitive model” that links brain and behaviour and forms a plausible and comprehensible alternative cognitive mechanism to associative models of cognition (e.g. Byrne and Bates 2006).

Unsurprisingly, I can offer no solution to this problem, nor was it my intent to differentiate between so-called low- and high-level mechanisms related to tool-use in woodpecker finches. For my part, I was interested in one particular subtlety of learning that is often glossed over in the literature: the bias of some animals to learn about certain types of information—in particular those which are relevant to a biological problem faced—more easily than others. One classical example is the predisposition of rats to develop a fast association between taste and illness (Garcia et al. 1966). Such predispositions presumably arise from the value of acquiring such information in a given animal’s natural environment. However, I did not aim to unravel the exact processes that underly this ability.

## **Comparative methods**

Two complementary approaches have traditionally been taken in attempts to compare cognition between species: the search for character divergence in closely related species under differing selective conditions and the search for convergence amongst unrelated species due to similar selective conditions (Shettleworth 1998). In order to demonstrate the association between traits such as tool-use and another character (e.g. a cognitive trait), we would ideally test as many independent tool-using/non-tool-using species pairs as possible because each pair only forms one data point.

The main goal of my thesis work was to improve our understanding of the link between tool-use and cognition through a controlled comparative investigation involving the tool-using woodpecker finch and the small tree finch, a closely related non-tool-using species: both species are members of the Darwin’s finch clade. There is no evidence suggesting that tool-use of woodpecker finches is linked with a cognitive sophistication on par with that of chimpanzees or New Caledonian crows. Nevertheless, enhanced cognition might have evolved in conjunction with tool-use that has high survival value. Other possibilities are that one or more cognitive abilities evolved in a different context and acted as a pre-adaptation facilitating the evolution of tool-use or finally it might be that cognition was not enhanced at all in conjunction with tool-use. Darwin’s finches are a perfect model with which to examine these questions, since one member of this group of 15 closely related species uses tools, and this species group as a whole has proven in the past to be ideal for the study of correlated evolution (Grant 1986).

## **THE DARWIN’S FINCHES OF THE GALÁPAGOS**

### **The Galápagos archipelago**

The Galápagos archipelago is home to all but one species of Darwin’s finch. The Galápagos is situated on the equator, approximately 950 km west of continental Ecuador. The island group is of volcanic origin and is composed of 13 larger islands (more than 10km<sup>2</sup>), 6 smaller

islands and over 40 islets. Although the Galápagos Islands are located on the equator, environmental conditions are harsh and unpredictable (Grant 1986). The Humboldt current brings cold water to the Ecuadorian coast which causes an unusually dry and highly seasonal climate, with a short rainy season from January to April and a dry season for the remainder of the year. Particularly at elevations near sea level, annual rainfall is low (0- 300 mm/year) (Hamann 1981). In addition to the annual climatic fluctuation in rainfall, the onset of the dry and wet season varies from year to year and the climate is strongly influenced by the irregular El Niño phenomenon which is characterised by unusually high sea temperatures and heavy rainfall. El Niño events are often followed by severe droughts which cause high mortality in finch populations (Grant and Boag 1980).

Since all studies on the woodpecker finch thus far have been conducted on the central inhabited island of Santa Cruz and because it is of relevance to the studies on woodpecker finch feeding ecology (Tebbich et al. 2002; Tebbich et al. 2004), I will describe the habitat composition of this island in some detail. This island stretches 800m above sea level. Here, as on all of the larger islands of the archipelago, distinct vegetation zones are situated along an altitudinal gradient stretching from deserts at or near sea level to lush cloud forest and moor land at high altitudes (Hamann 1981; Jackson 1993). Six distinct vegetation zones are characteristic of this island: the Coastal zone, the Arid zone, the Transitional zone, the Scalesia zone, the Brown zone and the Fern zone (made up of the Miconia and Pampa zones, Jackson 1993). The Arid zone and the Scalesia zone have been of particular focus in previous studies on the ecology of the woodpecker finch (Tebbich et al. 2002; Tebbich et al. 2004), the main reason being the dramatic difference in annual precipitation in these areas. This discrepancy leads to a stark difference in available food resources between the zones and consequently has a drastic effect on the ecology of the species inhabiting these zones.

The Arid zone begins just inland of the coast and extends up to an elevation of about 80-120 meters asl. It is covered by a semi-desert forest consisting of deciduous trees shrubs and cacti. The Scalesia zone ranges from 300-600m asl and is an evergreen cloud forest extending to the southern and eastern slopes of the island. Moisture evaporated from the sea is concentrated in an inversion layer at 300-600m asl and so it rains all year round in the Scalesia zone (Hamann 1981). This zone is dominated by the tree-like *Scalesia pedunculata*. Tree- trunks and branches in this zone are densely covered with epiphytes, mostly mosses.

Nine Darwin's finch species are found on the island of Santa Cruz. Of these, 5 species are found both in the Arid and the humid zones.

## Darwin's finches

I now turn to the Darwin's finches of which all except one species are endemic to the Galápagos islands. Depending on how they are classified, there are 14 or 15 species of Darwin's finches (Petren et al. 1999), 13 of which are confined to the Galápagos Archipelago and one (the Cocos finch, *Pinarolaxias inornata*) that is found on Cocos Island. The clade is com-

prised of 6 species of ground finches (genus *Geospiza*), and 5 species of tree finches (genera *Camarhynchus* and *Cactospiza*). Other species include the warbler finch (*Certhidea olivacea* and *C. fusca*)<sup>2</sup> which is most basal within the Darwin's finch phylogeny, the vegetarian finch (*Platyspiza crassirostris*) and the Cocos finch. True to their names, the ground finches often feed on the ground while the tree finches are mostly arboreal and more insectivorous.

Members of this group differ mainly in beak morphology which neatly reflects the various foraging niches into which the species have radiated (e.g. Grant 1986). The adaptive radiation of Darwin's finches took place rapidly and only recently in evolutionary history. It is thought that the ancestor(s) of all Darwin's finches arrived in the Galápagos from Central or South America approximately 2-3 million years ago (Grant and Grant 2008) and that the first split in this group occurred 1.6-2 million years ago (Petren et al. 2005). There is a lack of clarity on this point: according to Grant and Grant (2008), the radiation of Darwin's finches could have begun as early as 2.8 million years ago. Though no single extant mainland species can irrefutably claim the role of the closest living relative of Darwin's finches, three candidate genera have been proposed: *Tiaris*, *Melanospiza*, and *Loxigilla* (Burns et al. 2002). At least one study supports *Tiaris* as the most closely related genus and within this, the dull-coloured grassquit (*Tiaris obscura*) as the closest living relative of Darwin's finches (Sato et al. 2001).

This group is a well-suited model with which to pursue evolutionary questions concerning morphological and behavioural adaptation because of their continuing presence in the same geographic location at which they evolved, their easy habituation in captivity, their sufficient similarity to one another facilitating reconstruction of their routes of diversification and the fact that they inhabit various environments that periodically fluctuate, allowing not only for interpretation of adaptation under continuous but also varying ecological pressures (Grant and Grant 2008).

## Innovative feeding behaviours of Darwin's finches

The tool-use of woodpecker finches might be the most famous of the extraordinary feeding behaviours found in Darwin's finches but it is by no means the only unusual foraging behaviour of this clade. Indeed, perhaps as an adaptation to the inhospitable conditions of the Galápagos, Darwin's finches have developed a suite of unusual behaviours and use of food types that are highly unusual for passerines (Tebbich et al. 2010).

Due to strict regulations for the protection of Galápagos wildlife and the remoteness of some of the Darwin's finch populations, hardly anything is known about the ecological relevance and the underlying mechanisms of these extraordinary behaviours. The tool-use of

---

<sup>2</sup> Genetic evidence suggests that the warbler finch, which is currently classified as one species (*C. olivacea*), could actually be considered as two separate species (Petren et al. 1999).

the woodpecker finch is an exception because woodpecker finches occur on the inhabited island of Santa Cruz. Here, they are easily accessible for field studies and the necessary infrastructure for experimental testing in aviaries is available.

## The woodpecker finch

Woodpecker finches are a medium-sized (~ 20g) member of the group of tree finches within the Darwin's finch clade. They are mainly insectivorous but sometimes also feed on fruits and nectar (Tebbich et al. 2004). They are most famous for their habitual use of either cactus spines or twigs as tools (Eibl-Eibesfeldt 1961). Anecdotal observations of tool-using behaviour also exist for the warbler finch (Hundley 1963), the cactus finch (*Geospiza scandens*) (Millikan and Bowman 1967) and the mangrove finch (*Cactospiza heliobatis*) (Curio and



*Woodpecker finch (Cactospiza pallida) using a tool to probe into a substrate. Drawing by Sue Anne Zollinger.*

Kramer 1964) but habitual tool-use could not be confirmed by repeated observation or documentation in any of these species (Fessl et al. 2010; Tebbich et al. 2004).

Woodpecker finches occupy habitats ranging from the harsh and unpredictable coastal areas to a lush cloud forest at higher altitude where the availability of food resources is more stable. Findings concerning the frequency of tool-use in woodpecker finches strongly indicate that it is an adaptation to harsh and unpredictable conditions. Tebbich et al. (2002) found that woodpecker finches hardly ever used tools where food resources are stable, abundant and easy to access (Scalesia zone) but spent about half of their foraging time and obtained nearly 50% of their prey using tools in the Arid zone during the dry season. In contrast, they only used tools for 12% percent of their foraging time during the wet season.

Among the few tool-using species for which tool-use time budgets are available, woodpecker finches are certainly among the top tool-users in terms of frequency of tool-use (Mann et al. 2008). The time budgets compiled by Tebbich and colleagues also allowed a cost-benefit analysis of tool-use in woodpecker finches. This analysis showed that even though the foraging success proportional to time spent foraging was similar with tool-use and with other foraging techniques, tool-use was more profitable because prey obtained with tool-use was significantly larger and had a higher energy content (Tebbich et al. 2002).

The ecologically-dependent population differences in woodpecker finches' ability to use

tools was confirmed by our observations on the tool-use frequency of captive birds. All of the woodpecker finches that were captured in the Arid zone for this study quickly used tools in captivity while only a small percentage of birds of this species taken from the wet zone were ever seen to use tools even after more than one year in captivity. In Chapters 1 and 2, I explain the methodology that I used to categorize woodpecker finches as tool-users and non-tool-users.

Woodpecker finch tool-use is context-specific but not inflexible. In the wild, woodpecker finches are often observed to modify tools before using them by shortening them if they are too long and breaking off transverse twigs or leaves that could hinder the insertion of a twig into tree holes. In the laboratory woodpecker finches likewise modify tools to suit task requirements and also are able to select tools of the appropriate length to obtain an out-of-reach food reward (Tebbich and Bshary 2004).

On the flip side, tool-using behaviour in woodpecker finches has hard-wired components as shown by the finding that woodpecker finches which are raised without a tool-using model will nevertheless develop tool-use (Tebbich et al. 2001). This stands in contrast to at least some primates where several forms of tool-use develop via social learning (reviewed in Tomasello and Call 1997). However, a strong genetic foundation of tool-using behaviour does not necessarily undermine the possibility that learning (both social and asocial) plays a key role in developing functional tool-use in this species.

Asocial learning probably is important, both in the ontogeny and evolution of tool-use in woodpecker finches. In woodpecker finches, non-social individual learning improves the efficiency of tool-using behaviour in ontogeny (Tebbich et al. 2001). In the laboratory, five individuals developed aberrant tool-using techniques that seemed to arise through fast trial-and-error learning. It is interesting to note that the broods and parents used in this study came from the humid areas where tool-use is a rare occurrence. Nevertheless, all offspring developed tool-using techniques regardless of whether or not the parents were able to use tools. Thus, it seems that ontogenetic unfolding of this complex behaviour is determined by a very specific genetic component but is enhanced through individual learning (Tebbich et al. 2001).

Finally, Tebbich and colleagues (2001) found that the ability to learn tool-use is restricted to a sensitive period early in ontogeny: as adults, non-tool-using woodpecker finches were unable to learn the technique even when given multiple opportunities to observe a conspecific using tools. Thus, the variation in tool-use frequency in natural populations co-varies with habitat and might also be a function of learning opportunities early in ontogeny.

## **INVESTIGATING THE EVOLUTION OF TOOL-RELATED COGNITION IN THE WOODPECKER FINCH**

If tool-use is associated with enhanced cognitive abilities, the question arises whether they are an adaptation for tool-use or a by-product of other adaptations. Two evolutionary scenari-

os are possible. In the first scenario, tool-use may drive the evolution of information processing skills: if tool-use is highly beneficial for survival, then there should be selective pressure to improve performance. Thereby it is conceivable that both simple cognitive mechanisms such as fast instrumental learning and more sophisticated ones such as enhanced physical cognition might improve tool-using behaviour. Alternatively, cognitive abilities that evolved in other contexts might precede and facilitate the evolution of tool-use. For example, animals that are faced with food that is difficult to access or with an unpredictable environment may benefit from developing enhanced cognitive abilities. These can then be exapted for tool-use. In this scenario, a general cognitive competence such as behavioural flexibility will be found in tool-users but also in other closely related species that do not use tools. In Chapter 4 (Tebbich et al. 2010), I present evidence for the scenario that unusual behavioural flexibility preceded and facilitated the evolution of tool-use in woodpecker finches. A final possibility is, of course, that tool-use is not associated with enhanced cognitive abilities.

To investigate these questions, I implemented the traditional comparative framework in my thesis, focusing on the comparison between closely related tool-using and non-tool-using species but also making comparisons with distantly related species where comparative work was available. Though my single two-species comparison cannot be used to establish general patterns of association between tool-use and cognition, it forms a basis for further comparisons. My prediction was that if tool-use evolved in conjunction with enhanced cognitive abilities, there should be a divergence in cognition between closely related species that differ primarily in their ability to use tools (Chapters 1-2). To test this prediction, I compared the cognition of woodpecker finches with that of the closely related, non-tool-using small tree finch.

This species pair is well-suited for an inter-specific comparison of cognition because apart from the capacity to use tools, they are similar in terms of phylogeny, ecology and morphology which limits the effect of contextual variables in learning (e.g. Bitterman 1960). An additional opportunity to investigate the effect of tool-using experience on cognitive abilities was provided by the variation in the tool-using abilities of woodpecker finches (see above). These favourable conditions set the stage for my investigations. The combination of my findings with the existing data set on woodpecker finches and some of their relatives, moves us one step closer to the integration of all four of Tinbergen's levels of investigation, allowing us to paint a more comprehensive picture of tool-use in this species.

In Chapters 1 and 2, I implemented a method that is similar to Heyes' triangulation method in order to assess different types of learning abilities. However, my aim was to see whether there is a difference in learning according to the type of stimuli that are presented, that is whether woodpecker finches are biased to form associations when confronted with certain types of perceptual information that are relevant to tool-users but not others. This perceptual information in the physical tasks of Chapters 1 and 2 was linked to tool-use in a very direct way. Specifically, the problems involved the necessary functional spatial relationship between a reward and the tool used to move it (Cane task: Chapter 1, Experiment 3) and the

properties of continuous vs. discontinuous surfaces (Seesaw task: Chapter 1, Experiment 2; Trap tube tasks: Chapter 2, all experiments).

My goal was NOT to show that woodpecker finches are capable of abstracting concepts that cannot be explained by associative learning and generalisation. Thus, the “transfer tasks” that I used, were not designed to systematically exclude opportunities for simple perceptual learning cues as prescribed by triangulation method, rather the slight changes in presentation were effected in order to see if woodpecker finches display the ecologically relevant propensity not only to learn about certain types of cues that are most relevant to tool-use, but also how well they can generalise this to a variety of situations.

I included both general learning tasks and specialized tasks where a solution could have been based on sensitivity to the necessary functional spatial relationships between stimuli and where the functional relationship between a tool and food was important. I predicted that woodpecker finches should have been better at such tasks because tool-use might predispose them to learn about simple spatial cues, and in particular the spatial cues that are involved in tool-use, that is the functional relationship between a tool and a food reward. The general learning tasks were conducted to exclude the possibility that if woodpecker finches excelled in the specialized tasks, this could have been due to a general enhancement in learning capacity. I was interested in differences in learning during the initial learning phase but also in the ability to immediately transfer knowledge acquired in the initial task to other conceptually similar but perceptually differing versions of a task (transfer tasks). Thus, my goal was somewhat different than the usual quest to differentiate between low- and high-level cognitive mechanisms.

## THESIS OUTLINE

The unifying theme of my thesis is the link between evolution and tool-related cognition. While the first two chapters of this thesis implement a two-species comparison between a tool-using and non-tool-using Darwin's finch species (woodpecker finches and small tree finches, respectively) to test for cognitive divergence in tool-using and non-tool-using Darwin's finch species, in the second two chapters, consideration of the factors driving cognitive evolution in Darwin's finches is broadened from tool-use to other factors, in particular flexibility and the perseverance necessitated by extractive foraging.

In Chapter 1, I implemented four laboratory paradigms designed to test a breadth of learning abilities from very general ones to specific tool-related physical problems. A finding that woodpecker finches outperformed non-tool-using small tree finches in tool-related tasks but not in general learning tasks would have suggested the presence of a cognitive adaptive specialization in the physical domain of tool-use in woodpecker finches.

Chapter 2 reports experiments in which I compared the cognitive abilities of woodpecker finches and small tree finches with a widely used paradigm, the “trap tube”. A multitude of different tool-using species and some non-tool-using species have been tested with this para-

digm so there is abundant comparative data available. This task utilizes a novel problem to test an animal's sensitivity to general physical interactions. I expected tool-users to excel in this ability compared to non-tool-users. The variation of tool-using abilities amongst woodpecker finches furthermore provided the opportunity to tease apart whether enhancement of cognitive abilities in woodpecker finches is due to tool-using experience or simply to the genetic composition of a tool-user. It should be noted that there is some contention as to the utility of the trap tube task and also with respect to the cognitive abilities that it actually tests. In retrospect, I see the task critically and air some of my views in the discussion. For these reasons, the trap tube is presented in Chapter 2 while the other physical tasks are presented as a unit with the general tasks in Chapter 1.

Chapter 3 is based on findings from Chapter 1, namely the unexpected finding that the non-tool-using species outperformed the tool-using species in a task testing flexibility in simple associative learning. In Chapter 3, two issues are raised. The first is the possibility that another lifestyle difference between the members of the two-species comparison aside from tool-use, namely persistent, extractive foraging might have exerted a further cognitive selective pressure, leading one species (woodpecker finches) to be less flexible than the other. More specifically, the hypothesis is that flexibility in associative learning might be depressed in species such as the woodpecker finch that engage in persistent, repetitive foraging behaviours such as wood-pecking that are only rewarded after relatively long periods. The second issue raised is an important one in comparative research, namely consideration of a possible correlation between learning abilities and personality traits such as novelty responses (Shettleworth 1998; Webster and Lefebvre 2001).

The last chapter reviews evidence pertaining to the idea that behavioural flexibility, could explain the rapid and extensive radiation of Darwin's finches compared with other Galápagos lineages. In this final chapter, the tool-use of the woodpecker finch slips into a supporting role as one of several behavioural innovations found amongst Darwin's finches.

# CHAPTER 1

---



## **SOMETIMES TOOL-USE IS NOT THE KEY: NO EVIDENCE FOR COGNITIVE ADAPTIVE SPECIALIZATIONS IN TOOL-USING WOODPECKER FINCHES**

Teschke I., Cartmill E., Stankewitz S., Tebbich, S.  
(submitted to *Animal Behaviour*)

### **Abstract**

*The use and manufacture of tools has been considered to be cognitively demanding and thus a possible evolutionary driving factor of intelligence. Animal tool-use provides the opportunity to investigate whether the use of tools evolved in conjunction with enhanced physical cognitive abilities. However, success in physical tasks may simply reflect enhanced general learning abilities and not cognitive adaptations to tool-use. To distinguish between these possibilities, we compared general learning and physical cognitive abilities between the tool-using woodpecker finch (*Cactospiza pallida*) and its close relative, the small tree finch (*Camarhynchus parvulus*). Since not all woodpecker finches use tools, we also compared tool-using and non-tool-using individuals, predicting that domain-specific experience should lead tool-using woodpecker finches to outperform non-tool-users in a task that is similar to their natural tool-use. Contrary to our predictions, woodpecker finches did not outperform small tree finches in either of the physical tasks and excelled in only one of the general learning tasks, and tool-using woodpecker finches did not outperform non-tool-using woodpecker finches in the physical task closely resembling tool-use. Our data provide no evidence that tool-use in woodpecker finches has evolved in conjunction with enhanced physical cognition or that domain-specific experience hones domain-specific skills. This is an important contribution to a growing body of evidence indicating that animal tool-use, even that which seems complex, does not necessitate specialized cognitive adaptations.*

One of the fundamental issues in the study of human and animal cognition concerns the factors that drove the evolution of intelligence. The ability to use tools has played a long-standing role in this debate because it is thought to be cognitively demanding (e.g. Parker and Gibson 1977, but see also Hansell and Ruxton 2008). If tool-use poses a cognitive challenge and provides a selective advantage in acquiring resources, then we would expect that enhanced cognitive abilities should have evolved to increase the effectiveness of tool-use or to enable the development of such an unusual technique in the first place. The notion that tool-use should be linked to cognition related to learning about the physical world, for example the spatial relationships between objects, connectivity and weight, has been

particularly popular amongst cognitive biologists and has generated many studies of tool-related cognition in primates (Hauser et al. 1999; Martin-Ordas et al. 2008; Povinelli 2000; Santos et al. 2006; Seed et al. 2009; reviewed in Visalberghi and Tomasello 1998) and birds (e.g. Auersperg et al. 2009; Kacelnik et al. 2006; Seed et al. 2006; Taylor et al. 2008; von Bayern et al. 2009; Wimpenny et al. 2009; reviewed in Emery and Clayton 2009). Some of the strongest evidence supporting the notion that tool-use is linked to enhanced cognition is the strong correlation between tool-use and brain size in birds (Lefebvre et al. 2002) and primates (Reader and Laland 2002) as well as the demonstration that the cerebellum of tool-using birds has a higher degree of folding than that of non-tool-using birds (Iwaniuk et al. 2009). However, these findings provide only an indirect demonstration of the connection between tool-use and enhanced cognition and must be confirmed by behavioural experiments conducted in a comparative framework.

Several comparative methods are available to demonstrate that a given character, behaviour or cognitive trait is related to an ecological condition (e.g. Harvey and Pagel 1991; Shettleworth 1998). Traditionally, two approaches have been taken: the search for character divergence in closely related species under differing selective conditions and the search for convergence amongst unrelated species due to similar selective conditions. While these approaches are both necessary and informative by themselves, it is only through the synthesis of the two and by gathering repeated observations of the same pattern of convergence and divergence in several evolutionarily distinct groups that we can possibly begin to understand the true relationship between tool-use and physical cognition.

The woodpecker finch (*Cactospiza pallida*) is a tool-using species that habitually uses twigs or cactus spines to poke arthropods out of tree holes (Eibl-Eibesfeldt 1961). Experiments have demonstrated that juvenile woodpecker finches acquire the ability to use tools in distinct developmental stages independently of whether or not they are raised with a tool-using model, indicating that this ability is based on a specific genetic predisposition and is not dependent on social learning (Tebbich et al. 2001).

In this study, we compare cognition in woodpecker finches, a species that habitually uses tools, and the closely related non-tool-using small tree finch (*Camarhynchus parvulus*). These two Darwin's finch species are both members of the tree finch clade within the Darwin's finches and are found sympatrically throughout Santa Cruz Island of the Galápagos archipelago—these similarities minimize the influence of contextual variables as explanations for differences in cognitive abilities. The main objective of this study was to see whether this species pair shows a divergence in cognitive abilities apart from the genetic predisposition to acquire tool-use. Such cognitive divergence could be limited to evaluation of inputs from the domain of tool-use, for example, appreciation of the functional relationship between a tool and the object that it moves.

To test the hypothesis that tool-use in woodpecker finches co-evolved with enhanced physical cognitive abilities, we compared their performance with that of small tree finches in two tasks designed to test different aspects of physical cognition. The physical tasks can be

assigned into two sub-categories: one task required the passive use of tools where the birds only had to pull a tool (but were not required to perform any other manipulations on it) while the other task tested physical cognition but did not require the use of tools at all. Testing physical cognition with paradigms that involve the use of tools and ones that do not facilitates more precise specification of the level of adaptation, allowing us to determine whether tool-use evolved in conjunction with a general increase in physical cognition, or whether the cognitive adaptations are specific to problems related to the use of tools.

Those subjects that solved the initial problem posed by either of the physical tasks were subsequently tested in a series of transfer tasks in order to see whether they could transfer acquired knowledge to novel situations—an ability that is highly relevant in their natural feeding ecology. Typically, the goal of such transfer tasks is to differentiate dichotomously between high- and low-level cognitive solutions to a given problem. However in past studies that have adopted this approach, only a very small number of the tested animals (if any) succeeded in solving the entire task series. While this is useful in staking out the cognitive limits of a species, the low number of successful individuals also limits the opportunity of making quantitative comparisons. Thus, here we deliberately designed simple transfer task series which did not systematically preclude the use of all procedural rules instead of searching for a cognitive dichotomy.

In addition to the physical tasks, we also tested birds in two general learning tasks: one tested flexibility in learning while the other tested performance in a novel operant task. The purpose of including these general learning tasks was first and foremost to exclude the possibility that enhanced general learning abilities might explain competence in the specialized physical tasks but the tasks also provided us with clues as to what general learning abilities might differ between species and how this might fit into an explanation of the inter- and intraspecific patterns found in the specialized physical tasks.

In a previous paper addressing the role that unusual flexibility might have played in the adaptive radiation of Darwin's finches (Tebich et al. 2010), we reported that woodpecker finches do not outperform small tree finches in the two physical tasks and we proposed that perseverance in the foraging style of woodpecker finches may make them less sensitive to the absence of a reward which could negatively impact learning performance in these tasks. Here we present detailed analysis of the behaviour of both species to test this explanation of the results. Furthermore, in this study we present new analyses assessing the effect of tool-using experience in ontogeny on task performance and we discuss our findings in the context of general learning abilities.

The main prediction was: if tool-use evolved in conjunction with an adaptive specialization in the physical domain of tool-use in woodpecker finches, then this species should excel in the physical cognitive tasks, but not in general learning tasks. However, an outperformance of small tree finches by woodpecker finches could also be attributed to a disparity in tool-using experience and not to a more deeply rooted cognitive adaptation. For example, it is known that domain-specific experience improves performance in tasks testing domain-

specific tool-related cognitive abilities in non-human primates (Hauser et al. 2002; Spaulding and Hauser 2005). Since not all woodpecker finches acquire the technique of tool-use in their lifetime, we were presented with a unique opportunity to investigate how domain-specific experience with tools influences the physical cognitive abilities within this species. Woodpecker finches from different habitats vary in their ability to use tools as adults. These differences can be attributed to differences in seasonal fluctuations in food availability: woodpecker finches obtain about half of their prey using tools in arid habitats during the dry season while those birds inhabiting humid areas hardly ever use tools (Tebbich et al. 2002). Moreover, adult woodpecker finches that do not use tools do not acquire the technique in adulthood even with extensive tool-use tutoring by a conspecific (Tebbich et al. 2001).

We used this natural variation to tease apart species competence and individual ability honed by experience in physical task performance while at the same time controlling for the effects of enhanced general learning. Since the species comparison and the investigation of the effect of ontogeny on physical cognition are not separable, we modified our main predictions for the physical tasks by taking ontogeny into account. The new predictions were: if there is a cognitive adaptation that evolved in conjunction with tool-use in woodpecker finches, then we would expect both those woodpecker finches with and without tool-using experience to outperform small tree finches and furthermore, if experience hones physical cognition, then tool-using woodpecker finches should perform best of all. Additionally, if the adaptation is specialized for physical cognition, then neither group of woodpecker finches should excel compared to small tree finches in the general learning tasks. However, if there is no cognitive adaptation that evolved with tool-use in woodpecker finches, then we would expect both woodpecker finch groups to perform similarly to small tree finches in the physical tasks. Finally, it is possible that experience alone might improve the performance of tool-using woodpecker finches in which case we would expect only tool-using woodpecker finches to outperform small tree finches in physical tasks but not non-tool-using ones.

To our knowledge, this is the first fully controlled comparison of physical- and general cognitive abilities between closely related tool-using and non-tool-using species in which both species have been tested in parallel using identical experimental paradigms. This study will permit us to draw conclusions about the interactions between tool-use and cognitive abilities on both ontogenetic and evolutionary time scales.

## **METHODS**

### **Study area, subjects and housing**

The study was carried out at the Charles Darwin Research Station on Santa Cruz Island in the Galápagos Archipelago, Ecuador from October 2007 - March 2008 and September 2008 - January 2009. A total of 18 woodpecker finches and 16 small tree finches were mist-netted for this study. Following capture, finches were first kept in a small habituation cage (0.5 x 0.5

x 1m) for  $\leq 5$  days. Thereafter, the birds were maintained in outdoor aviaries (3.92 x 3m or 2 x 1 x 2m). Aviaries were furnished with natural branches and an experiment table on which the apparatus were presented.

Birds were kept singly and visually isolated from each other on a diet of mashed hard-boiled egg, grated carrot, mixed with commercial bird food mix (Orlux®). Additionally, the birds received fresh fruit and fresh moths daily following testing. Subjects were kept at 100% of their free-feeding weight. Not all birds participated in all experiments. A summary clarifying the order of experiments and the participation of each bird in each experiment is given in Appendix 1. Tool-using ability of woodpecker finches was always assessed prior to participation in experiments (Appendix 2, Section 1.2).

## **Ethical Note**

Permission to conduct this study was granted by the Galápagos National Park and the Charles Darwin research station (Project PC-16-07, Permit Nr. PR.PT.P004.R02). Further ethical information may be found in Appendix 2 (Section 1.1).

## **Basic experimental procedure**

Experiments were conducted in the home aviaries of the birds and food was removed from their aviaries 2 hours preceding testing. Apparatus were always baited out of sight of the subject and for each trial, placed onto the experimental table within the home aviary. The experimenter then left the room and observed the trial via a camcorder (JVC GZ-MG130EK hard disk camcorder). All experiments except Experiment 2 were recorded with the camcorder.

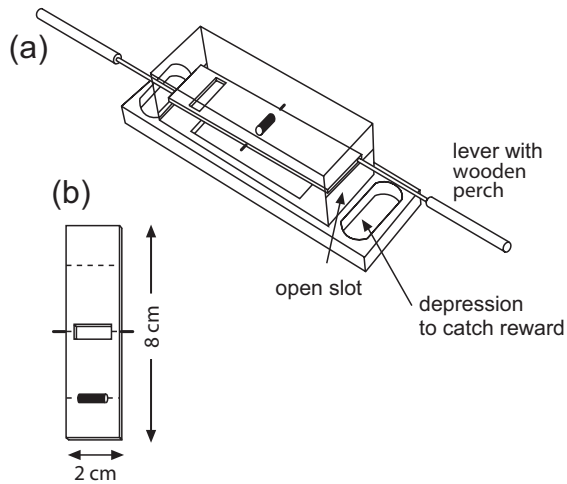
### ***Experiment 1: The reversal task (general learning)***

This experiment consisted of two phases: an initial “acquisition phase” and a “reversal phase”. In the acquisition phase, subjects were given a choice between two lids of different colours (orange and blue), one of which was the rewarded S+ stimulus. Once a subject met criterion (see “experimental procedures”) in the initial colour discrimination, the colour-reward contingency was reversed in the reversal phase.

The apparatus consisted of 2 feeders covered with coloured lids that were mounted 10 cm apart on a wooden base. In each trial a reward was placed in one of the feeders, the lids were placed on the feeders and birds were then allowed to remove one of the two lids. A transparent Perspex divider prevented the birds from removing the lid of both feeders. Eight small tree finches, 6 non-tool-using and 10 tool-using woodpecker finches were tested in this experiment. In the acquisition phase of the reversal task, 1 non-tool-using woodpecker finch was mistakenly stopped after not having reached full criterion (logistic regression line with

negative slope in Figure 1.4a, middle row). Since this did not affect our main conclusions, we retained the data point in the analysis.

### **Experiment 2: The seesaw task (physical non-tool-use)**



**Figure 1.1** The seesaw apparatus. (a) The seesaw task apparatus depicted in the Food-central condition and (b) the Gap-central condition.

This task was designed to test sensitivity to surface continuity. However, the initial task could also be solved using the spatial relationship between elements of the task. The apparatus consisted of a spring-loaded, horizontal seesaw platform encased in a clear Perspex box (Figure 1.1).

Perch-levers were attached to the left and right side of the seesaw so that the platform could be tilted by perching on either lever. A reward encased in clear plastic tubing rested on the seesaw at the beginning of each trial. Perching on either of the levers caused the reward to roll down the length of the platform toward the bird (Movie A6, Appendix 6).

The seesaw platform always contained a hole (gap) and an error was made when the bird tilted the platform so that the food rolled into the hole and was inaccessible. In contrast, birds were rewarded when they perched on the side that caused the food to roll down the continuous portion of the seesaw platform and out of the apparatus. Six small tree finches, 6 non-tool-using and 6 tool-using woodpecker finches participated in this experiment.

**Initial task** There were two conditions in this experiment: Food-central and Gap-central (Figure 1.1a,b). Upon solving the initial task, a bird was subsequently presented with the unfamiliar condition as the transfer task.

**Apparatus malfunctions** In 2.7% of trials during the initial task, the apparatus malfunctioned, meaning that the birds sometimes were not rewarded when they should have been or were rewarded when they should not have been (summary in Appendix 3, Table A3.1). In most cases extra trials were given to the birds that experienced such problems as compensation. Though we found no significant relationship between malfunction rate and success (Section 2.1 of Appendix 2 contains details and results), we nevertheless excluded trials in which the apparatus malfunctioned from the GLMM analyses (see statistical analysis below).

### *Experiment 3: The cane task (physical tool-use)*

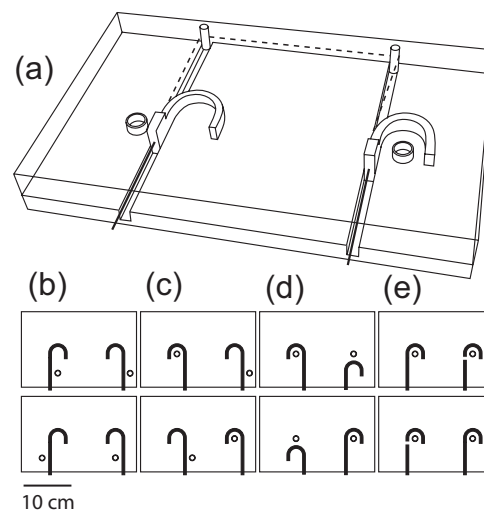
This experiment involved food retrieval contingent on making a choice between two canes, only one of which could retrieve the reward, and was designed to investigate subject's sensitivity to the functional relationship between a reward and the tool used to attain it. In each condition, one food reward was inside the hooked portion of the cane and one outside of it (with the exception of transfer task 4 in which both rewards were inside the hooked portion of both canes) and the reward could only be retrieved by pulling the cane in the correct functional relationship with the food (Figure 1.2 and Movie A6, Appendix 6). Each cane was fitted into a groove so that they could only be pulled forward in a straight line and could not be flipped.

Also, the canes were attached to one another by a string which was threaded around two spindles at the back end of the apparatus (Figure 1.2a). This ensured that pulling one cane caused the other to simultaneously retract into the apparatus, thus imposing a mild form of forced-choice. The entire apparatus was covered with a clear Perspex lid so that the food and canes were visible from above but the food could not be reached until it had been pulled out from underneath the lid.

Six small tree finches, 6 non-tool-using and 6 tool-using woodpecker finches participated in this experiment.

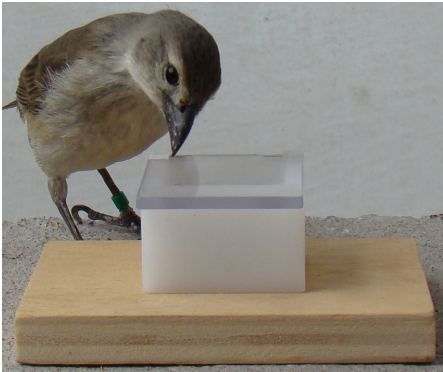
**Transfer tasks** Those subjects that solved the initial version of the task were then tested in 4 further variations of the initial task (transfer tasks: Figure 1.2b-e).

**Erroneous configurations in first transfer task** During the first session of the first transfer task, 4 birds (2 small tree finches, 1 non-tool-using- and 1 tool-using woodpecker finch) inadvertently received 4 – 10 trials that did not conform with the intended configuration of this task. In all cases, it was likely that the erroneous configurations should have made it easier for the birds to solve the task. However, none of them reached the success criterion or even approached it in their first session and the birds were subsequently given an extra block of the first transfer task to make up for the erroneous first session.



**Figure 1.2** (a) The cane task apparatus with canes and rewards arranged as in the initial test condition. (b)- (e) Transfer tasks 1-4 (first row: left-hand side is correct option, second row: right-hand side is correct).

### *Experiment 4: The novel box opening task*



**Figure 1.3** Woodpecker finch in box opening task. From above, the bird can see the food reward inside.

This task was meant to test the ability to solve a novel operant task. The apparatus was a box made of opaque, white Perspex with a transparent lid. The lid was hinged to the back edge of the box and overlapped the front edge of the box (Figure 1.3).

The box could be opened by pushing the protruding lip of the lid upwards. Before testing, birds were habituated to the box by feeding from it once while it was open. Subjects were given 6 sessions of 25 min. and received up to 3 sessions per day. A bird was successful and testing was ended when it opened the box and ate the reward. If a bird did not contact the box during a session, it was re-habituated to the box as

described above and the session was repeated. A bird was given up to 2 extra sessions upon failing to make contact with the box in any one session. Eight small tree finches, 8 non-tool-using and 10 tool-using woodpecker finches participated in this experiment.

We scored the following variables from video footage for each individual: “latency to contact the box in first session” (seconds), “frequency of box contacts”, “total length of testing (in seconds)” and “success” (opening box and gaining access to the food reward).

**Modified box opening task** Five small tree finches that failed in the original task were presented with a modified version of the task. This box was the same as the original except that the box sides were transparent and the lid was opaque. Here, the birds could see the food from the side, increasing the likelihood that they would accidentally nudge the lid upwards with their head, thereby solving the problem. We presented this modified box to control for the possibility that the small tree finches’ inability to solve the original problem was due to lack of physical strength.

## **Procedures and analysis of two-choice experiments (Experiments 1-3)**

### *Experimental procedures*

Experiments 1-3 were two-choice learning experiments involving the same basic procedure. These tasks were conducted in blocks of 10 trials. In each trial, the subject was given 5 min. to make a choice between two options for which the correct side was randomized and counterbalanced right and left. Where there was more than one condition in the initial phase (Experiments 1 and 2), starting conditions were balanced according to test groups.

**Success criterion** In the initial task, subjects were given at least 140 trials to meet the success criterion. In the physical tasks, subjects that solved the initial task were subsequently tested in one or more transfer tasks. Since the emphasis here was on what the birds could immediately apply to the new version of the problem, birds were only given up to 30 trials to meet criterion in the transfer tasks. In the reversal task (Experiment 1), there were two testing phases and the birds were given 140 trials to meet the success criterion in each phase.

To meet the success criterion, a bird had to make 15 or more correct choices within two consecutive blocks of 10 trials. Specifically, the number of correct responses in one of the two blocks had to be at least 7 consecutively correct and in the other at least 8, or in one block all 10 correct. This criterion was derived using a Monte Carlo simulation (details in Tebbich et al. 2007). Further details of the experimental procedure are given in Appendix 2 (Section 1.3).

**Side bias correction** Some subjects developed a positional bias, probably as a result of intermittent reinforcement. When a subject developed a positional bias, defined as 6 consecutive choices of one side, we employed a side bias correction procedure (“correction trials”) until that subject chose the non-preferred side once, whereupon we reverted to the normal pseudo-randomized trial schedule.

### *Data analysis*

For all experiments, Fisher’s exact test was used to test for group differences in the proportion of individuals to successfully meet the success criterion (see above). If this test did not show a significant difference between tool-using and non-tool-using woodpecker finches we pooled these groups and compared the pooled woodpecker finches with small tree finches.

We also compared learning speed and success probability between groups (“group” = small tree finches, tool-using woodpecker finches, non-tool-using woodpecker finches) in the initial phases of the seesaw and cane tasks and for both phases of the reversal task using Generalized Linear Mixed Models (GLMM, Baayen 2008). To this end, a separate model was constructed for the initial phase of each experiment (and for each phase of the reversal task). Initial (full) models always included “group” and “trial number” as fixed effects and “subject” as a random effect as well as the interactions between fixed effects up to the second order (Section 2.2 of Appendix 2 contains details). The full model for the seesaw task also incorporated “condition”, referring to testing condition in the initial task (gap-central vs. food-central), as a fixed effect. Finally, to control for possible subject differences in learning speed, each model also included random slopes in addition to random intercepts (Schielzeth and Forstmeier 2009).

GLMMs were fitted in R (R development core team 2009, R version 2.9.1) using the function `lmer` of the R package `lme4` (version 0.999375-31, Bates and Maechler 2009). Because the response variable was binary (success/failure), we specified binomial errors and

the “logit” link function. Likelihood ratio tests were used to compare models.

We were primarily interested in the interaction between trial number and group since a significant interaction between these factors would have indicated that groups learned at different speeds. A significant main effect of group indicated that groups differed in their overall probability to choose successfully, a main effect of condition for the seesaw model indicated that one condition was easier to learn than the other, while a main effect of trial number simply indicated overall learning.

Prior to analysis, side bias correction trials were removed from all data sets and trials in which the seesaw apparatus malfunctioned were excluded from the seesaw data set. Some model results are reported in the main text (but see Appendix 3, Tables A3.2-A3.4 for full results).

Recently it has been argued that the reliability of p values associated with fixed effects is questionable in the context of mixed models (Bolker et al. 2009). We therefore always backed up our conclusions with analysis of an alternative measure of learning speed, (“point of steepest slope” calculated for each individual using the coefficients derived through logistic regression, Appendix 2, Section 2.3) and an alternative measure of overall success probability (“percent errors” for each individual) using one-way ANOVAs and the non-parametric Kruskal-Wallis test. The results of these analyses are only reported in the main text when they did not confirm the GLMM results (descriptive statistics and full results are contained in Tables A3.5-A3.8).

**Analysis of perseverance in the two-choice experiments** In a recent paper (Tebbich et al. 2010), we proposed that perseverance in the natural feeding ecology of woodpecker finches, which often requires long bouts of pecking that are only rewarded after relatively long periods, might lead to a natural insensitivity to non-reward which could hinder their learning capacities and explain the fact that they were unable to outperform small tree finches in our two-choice learning experiments. Here we attempted to test this idea by looking at the perseverance with which woodpecker finches continue a positional bias when such a strategy yields 0% success, namely while the side bias correction procedure of the two-choice learning tasks is being implemented. To this end, we examined sequences of choices to one side during application of the side bias correction procedure, asking a) whether any of the groups persisted in choosing the non-rewarded side in a significantly higher percentage of trials than the others and b) whether there were differences in the mean length of side bias correction sequences. A “sequence” was defined as one or more consecutive choices of the biased side during the correction procedure, that is, following 6 consecutive choices to one side in which an individual were rewarded approximately in 50% of trials for this strategy, and breaks between sessions were disregarded.

For each individual, we calculated the percentage of total trials given during the side bias correction procedure and the mean correction sequence length by dividing the total number of side bias correction trials by the total number of side bias sequences. These two response

variables were analyzed using one-way ANOVAs with “group” (“group” = small tree finches, tool-using woodpecker finches, non-tool-using woodpecker finches) as the explanatory variable. The analyses were conducted separately for each task since not all birds were tested in all tasks.

Before applying the ANOVA test, data were tested for homogeneity of variance using the Bartlett’s test (Snedecor and Cochran 1989) and the Fligner-Killeen test (Conover et al. 1981). If either of these tests indicated a departure from homogeneity of variance ( $p < 0.05$ ), transformations were performed on the data in question, the best transformation was selected and the one-way ANOVA was then performed on the transformed data. Otherwise, testing was always performed with the original data and a Kruskal-Wallis test was always used to back up results. A summary of the statistical tests is given in Table 1.1 and descriptive statistics for the perseverance data are in Table 1.2.

## RESULTS

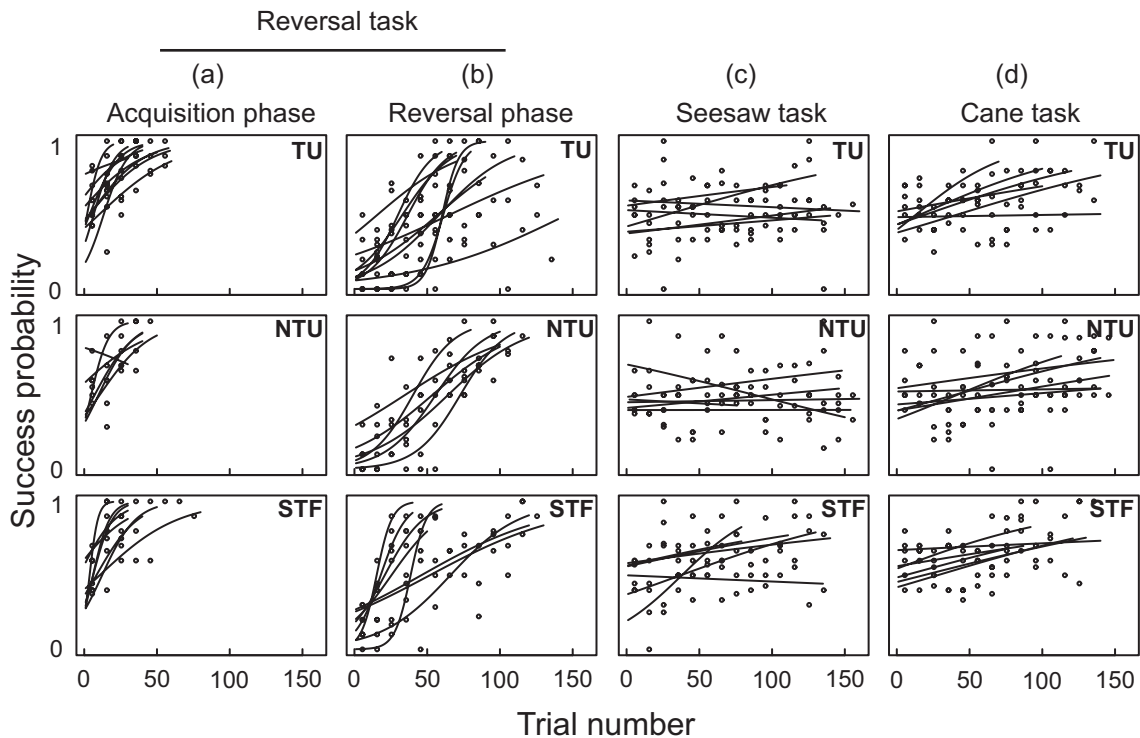
### Experiment 1: The reversal task

All individuals met criterion in the acquisition task within 80 trials or less and all except one, met criterion during the reversal task in less than 140 trials. Thus, we did not test for group differences in the proportion of successful individuals.

Groups did not differ in their speed of learning either in the acquisition phase (acquisition phase model, group\*trial number:  $\chi^2 = 0.18$ ,  $df = 2$ ,  $p = 0.916$ , Figure 1.4a) or in the reversal phase (reversal phase model, group\*trial number:  $\chi^2 = 0.55$ ,  $df = 2$ ,  $p = 0.761$ , Figure 1.4b) though individuals clearly learned in both phases of the task (acquisition phase model, trial number:  $z = 8.315$ ,  $p < 0.0001$ , reversal phase model, trial number:  $z = 8.597$ ,  $p < 0.0001$ ). Though the overall success probability did not differ between groups in the acquisition phase (group:  $\chi^2 = 0.18$ ,  $df = 2$ ,  $p = 0.915$ , Figure 1.4a), there was a significant difference between groups in the reversal phase (reversal phase model, group:  $\chi^2 = 6.18$ ,  $df = 2$ ,  $p = 0.046$ , Figure 1.4b). Small tree finches had a significantly higher success probability than non-tool-using woodpecker finches ( $z = 2.24$ ,  $p = 0.025$ ) and tool-using woodpecker finches ( $z = -2.18$ ,  $p = 0.029$ ) but there was not a significant difference between tool-using and non-tool-using woodpecker finches ( $z = 0.21$ ,  $p = 0.832$ ). The main effect of group was confirmed as a trend by the ANOVA and Kruskal-Wallis tests of percent errors by group (one-way ANOVA:  $F_{2,21} = 3.11$ ,  $p = 0.065$ ; Kruskal-Wallis test:  $\chi^2 = 5.17$ ,  $df = 2$ ,  $p = 0.076$ ).

### Experiment 2: The seesaw task

**Initial task** Of the 6 tool-using and 6 non-tool-using woodpecker finches tested in the initial seesaw task, only 2 tool-using and no non-tool-using woodpecker finches solved it (Fisher’s exact test:  $p = 0.454$ ). A significantly higher proportion of small tree finches (5 of the 6) than



**Figure 1.4** Logistic regression models of success probability across trial number for two-choice learning tasks. Models of success probability for the reversal task [(a) acquisition phase and (b) reversal phase], the seesaw task (c) and cane task (d). Each row refers to one of the three test groups (top: TU= tool-using woodpecker finches; middle: NTU= tool-using woodpecker finches; bottom: STF=small tree finches). Points refer to the proportion of correct trials per block of 10 trials for each individual.

pooled woodpecker finches reached the success criterion in the initial seesaw task (Fisher's exact test:  $p = 0.013$ ).

Groups did not learn at significantly different speeds (group\*trial number:  $\chi^2 = 4.29$ ,  $df = 2$ ,  $p = 0.117$ , Figure 1.4c) but there was a significant difference in the overall success probability (group:  $\chi^2 = 8.85$ ,  $df = 2$ ,  $p = 0.012$ ) with small tree finches having a significantly overall higher success probability than non-tool-using woodpecker finches ( $z = 3.50$ ,  $p < 0.001$ ) but not than tool-using woodpecker finches ( $z = -1.34$ ,  $p = 0.181$ ). Furthermore, there was no significant difference between tool-using and non-tool-using woodpecker finches ( $z = 1.43$ ,  $p = 0.153$ ). Overall, subjects tended to improve over the sequence of trials (trial number:  $z = 1.85$ ,  $p = 0.065$ ) with the suggested increase being seemingly similar in all groups. Interestingly, subjects made fewer errors in the Gap-central condition than in the Food-central condition ( $z = 4.125$ ,  $p < 0.001$ ).

**Transfer performance** Five of 6 small tree finches and 2 of 12 woodpecker finches (both tool-users) advanced to the transfer task. None of these birds passed the transfer task.

**Table 1.1** Test statistics comparing perseverance by group in terms of (a) percent correction trials and (b) mean correction sequence length for the initial phases of the seesaw and cane tasks and both phases of the reversal task.

	Reversal task		Seesaw task	Cane task
	Acquisition phase	Reversal phase		
<i>(a) Percent correction trials</i>				
<b>one-way ANOVA test<sup>1</sup></b>	$F_{2,21}=1.04,$ $p=0.371$	$F_{2,21}=0.88,$ $p=0.428$	$F_{2,15}=0.48, p=0.630$ <i>cosine</i>	$F_{2,15}=2.31,$ $p=0.134$
<b>Kruskal-Wallis test</b>	$\chi^2=3.02, df=2,$ $p=0.221$	$\chi^2=1.24, df=2,$ $p=0.537$	$\chi^2=0.80, df=2,$ $p=0.671$	$\chi^2=3.52, df=2,$ $p=0.172$
<i>(b) Correction sequence length</i>				
<b>one-way ANOVA test</b>	<i>no appropriate transformation</i>	$F_{2,21}=0.69,$ $p=0.514$	$F_{2,15}=0.58, p=0.574$ <i>1/log</i>	$F_{2,15}=3.26,$ $p=0.067$ <i>square root</i>
<b>Kruskal-Wallis test</b>	$\chi^2=3.20, df=2,$ $p=0.202$	$\chi^2=1.06, df=2,$ $p=0.590$	$\chi^2=0.88, df=2,$ $p=0.643$	$\chi^2=5.11, df=2,$ $p=0.078$

<sup>1</sup> If the data did not meet the criterion for homogeneity of variance (criterion given in main text), the data was transformed until a suitable transformation was found. In this case, the ANOVA was conducted with the transformed data, and the transformation used is given underneath the results in italics, otherwise, the test was performed on the original data. If no suitable transformation could be found, only a Kruskal-Wallis test was performed. All transformations were performed on the response variable and the 1/log transformation was performed on the response variable with 1 added to each data point.

### Experiment 3: The cane task

**Initial task** Eight of 12 woodpecker finches (3 non-tool-users and 5 tool-users) and all 6 small tree finches attained the success criterion in this task. Testing showed that there was no significant difference either in the proportion of tool-using and non-tool-using woodpecker finches to reach criterion in the initial task (Fisher's exact test:  $p = 0.545$ ) or in the proportion of pooled woodpecker finches and small tree finches to solve the task (Fisher's exact test:  $p = 0.245$ ). The speed of learning did not differ between groups (group\*trial number:  $\chi^2 = 0.76, df = 2, p = 0.683$ , Figure 1.4d) but overall, birds improved their performance over the sequence of trials (trial number:  $z = 5.31, p < 0.0001$ ). Interestingly, the overall success probability differed between groups ( $\chi^2 = 6.91, df = 2, p = 0.032$ ), with small tree finches outperforming non-tool-using woodpecker finches ( $z = 2.90, p = 0.004$ ), but not tool-using woodpecker finches ( $z = -1.26, p = 0.209$ ). There was no significant difference between the two woodpecker finch groups ( $z = 1.61, p = 0.107$ ). This was confirmed as a trend by the ANOVA test of proportional errors by group ( $F_{2,15} = 3.54, p = 0.055$ ) but not by the Kruskal-Wallis ( $\chi^2 = 4.25, df = 2, p = 0.120$ ).

Table 1.2 Descriptive statistics quantifying perseverance by group in terms of percent correction trials and mean correction sequence length. for the initial phases of the seesaw and cane tasks and both phases of the reversal task by group

Group <sup>1</sup>	Reversal task		Seesaw task	Cane task
	Acquisition phase	Reversal phase		
<i>Percent correction trials (mean ± S.E.M.)</i>				
TU	10.50 ± 1.85	12.29 ± 3.18	20.47 ± 5.59	5.49 ± 1.87
NTU	9.47 ± 4.71	13.83 ± 5.76	30.14 ± 10.60	15.44 ± 4.90
STF	5.14 ± 2.69	7.17 ± 2.15	15.75 ± 3.09	10.86 ± 2.18
<i>Correction sequence length (mean ± S.E.M.)</i>				
TU	2.60 ± 0.37	4.04 ± 1.03	5.20 ± 0.95	1.61 ± 0.38
NTU	2.92 ± 1.72	3.97 ± 1.63	9.86 ± 5.07	4.92 ± 1.64
STF	1.47 ± 0.75	2.38 ± 0.87	3.97 ± 0.64	3.29 ± 0.57

<sup>1</sup> NTU = non-tool-using woodpecker finch, TU = tool-using woodpecker finch, STF = small tree finch

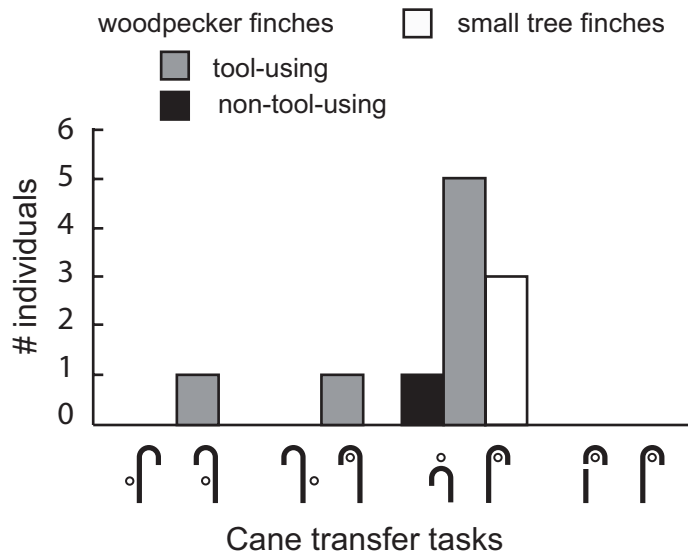


Figure 1.5 Cane task transfer performance. Performance given as the number of successful subjects of each group in each transfer task. The configuration of cane and reward configurations for transfer tasks 1-4 are shown beneath the graph from left to right. Each of these diagrams shows the configuration for a trial in which pulling the right-hand cane would be correct.

**Transfer performance** The 5 tool-using and 3 non-tool-using woodpecker finches and the 6 small tree finches that solved the initial task were subsequently tested in 4 transfer tasks. Only 1 subject, a tool-using woodpecker finch, met criterion in the first and second transfer tasks (Figure 1.5). In the third transfer task, 3 small tree finches and 6 woodpecker finches (5 tool-users and 1 non-tool-user) met criterion, whereas no birds solved the fourth task.

Detailed analysis of the one tool-using woodpecker finch that passed three of the four transfer tasks showed that this bird might have reached success by employing a trial-and-error strategy: it switched between canes in a higher percentage of all its transfer trials (58.9 %) compared to the mean ( $\pm$  S.E.M.) percent of transfer trials in which all other birds switched between canes in their transfer trials ( $7.4 \pm 1.4$  %), and 71.7 % of the transfer trials in which this bird switched between canes were correct though there was not a significant relationship between switching and success for this bird ( $\chi^2 = 0.176$ ,  $df = 1$ ,  $p = 0.675$ ).

## Experiment 4: The novel box opening task

Of the 18 woodpecker finches and 8 small tree finches tested in this task, 4 non-tool-using and 4 tool-using woodpecker finches successfully opened the box while none of the small tree finches were successful in doing so (comparison of the proportion of successful pooled woodpecker finches and small tree finches, Fisher's exact test:  $p = 0.031$ ).

Small tree finches were slower to contact the box in their first session (median = 133 seconds, range = 31-1500) than woodpecker finches (median = 30 seconds, range = 6-1500; Mann-Whitney U-test:  $U = 33$ ,  $N_{sf} = 8$ ,  $N_{wf} = 18$ ,  $p = 0.030$ )<sup>1</sup> and they contacted the box less frequently (median = 1.27 contacts/min., range = 0.49-2.93) than woodpecker finches (median = 2.32 contacts/min., range=0.49-25.24; Mann-Whitney U-test:  $U = 31$ ,  $N_{sf} = 8$ ,  $N_{wf} = 18$ ,  $p = 0.022$ ).

**Modified box opening task** Four out of 5 small tree finches solved the modified version of the box opening task within 6 sessions, with 2 of the birds even solving it in less than 40 seconds.

## Analysis of perseverance in the two-choice experiments

We found no evidence for a difference between groups in perseverance as measured by the percentage of side bias trials in either phase of the reversal task nor in either of the physical tasks (Table 1.1a). Furthermore, there was not a significant difference in the mean length of side bias sequences in the reversal phase of the reversal task nor in the initial phase of the seesaw task (Table 1.1b). A suitable transformation could not be found for the mean

---

<sup>1</sup> For all Mann-Whitney U-tests, the sample sizes of the comparison groups are given with a subscript denoting species group (sf=small tree finches, wf=woodpecker finches).

correction sequence length of the acquisition phase of the reversal task but the non-parametric Kruskal-Wallis test suggested that there was not a significant difference between groups. There was a trend for a significant difference in groups in the initial phase of the cane task (one-way ANOVA with square root-transformed data:  $F_{2,15} = 3.26, p = 0.067$ ). All summary and test statistics for this analysis can be found in Tables 1.1 and 1.2.

## DISCUSSION

Overall, our experiments provide no evidence that tool-use in woodpecker finches evolved in conjunction with enhanced physical cognitive abilities, nor did we find any clear evidence indicating that tool-using experience in woodpecker finches hones physical cognitive abilities. Neither tool-using nor non-tool-using woodpecker finches outperformed small tree finches in either of the physical tasks, nor did tool-using woodpecker finches outperform non-tool-using conspecifics in any of the tasks. In fact, contrary to our expectations, small tree finches outperformed woodpecker finches in some aspects of both physical tasks: significantly more small tree finches than woodpecker finches solved the seesaw task, and in both of the physical tasks, small tree finches made the fewest errors overall, though this difference was only significant with respect to non-tool-using woodpecker finches. The competence of small tree finches in the cane task was particularly surprising since the underlying physical problem presented in this task, namely sensitivity to the functional spatial relationship between tool and reward, is such an ecologically relevant one for tool-using woodpecker finches in the wild. Despite the adept performance of the non-tool-using species, the fact that individuals clearly found it easier to solve one condition of the seesaw task than the other illustrates the important role that attendance to simple cues (in this case, probably proximity to the food) played for both species in solving even physical tasks.

The only task in which woodpecker finches outperformed small tree finches was the box opening task: only woodpecker finches were able to solve this task because they made significantly more contact with the box. In a previous publication (Tebbich et al. 2010), we speculated that woodpecker finches' success in the box opening task might be due to their extractive foraging ecology, since their long bouts of energetic pecking at wood to gain access to a prey item should require them to be unusually persistent. Additionally, such perseverance might also be advantageous in the evolution and ontogenetic development of tool-use in woodpecker finches because acquiring and practicing tool-use successfully probably requires a high level of perseverance. In particular, it is known that extracting a prey item with tools takes significantly longer than using a conventional foraging technique (Tebbich et al. 2002). On the flip side, we also proposed that such perseverance might impede learning flexibility in the two-choice learning tasks because high perseverance is likely to be associated with a low sensitivity to absence of reinforcement (Tebbich et al. 2010). To test this notion, we assessed whether woodpecker finches are less sensitive to non-reward by analyzing the number and average length of side bias correction sequences by group. We could not

confirm this prediction: there was no significant difference between groups in the percentage of correction trials relative to the total number of trials nor in the mean length of sequences in which individuals persisted in choosing one side.

The direct statistical comparisons between tool-using and non-tool-using woodpecker finches did not yield evidence hinting at an improvement of physical cognition via experience. However, other aspects of our analysis suggest that such experience might still bring about quite subtle differences in physical task performance. For one thing, we consistently find that small tree finches are significantly better in the physical tasks (make fewer errors overall) than non-tool-using woodpecker finches but not tool-using ones. Furthermore, in the cane task, the only bird that solved all three transfer tasks was a tool-user, which suggests that this tool-using individual might have learned a more general rule. A close analysis of this bird's behaviour indicated that it applied a strategy involving observation of the moment-to-moment effect of its cane pulling actions on the movement of the reward, and therefore was not able to assess the solution in advance. It is possible that such a heuristic strategy is improved by tool-using experience, but on the basis of one bird, we cannot say for sure whether this is the case. To more fully examine the relationship between experience and cognition, a larger sample size of tool-using and non-tool-using woodpecker finches is needed.

Though we did not find an enhancement of either sensitivity to the functional spatial relationship between tool and reward (Cane task) or an appreciation of surface continuity (Seesaw task) in tool-users, it is possible that future work will demonstrate a connection between tool-use and other cognitive abilities not covered in the current study. One possibility is that woodpecker finches have enhanced cognitive abilities which are specific to active tool-use but for obvious reasons we were unable to assess this in a comparison with a non-tool-using species.

The fact that small tree finches outperform woodpecker finches in one of the general learning- and even the physical tasks alters our concept of tool-use in woodpecker finches and highlights the importance of investigating character divergence in closely related species. While a comparison between distantly related tool-using species indicated that the capacity to solve physical problems evolved in conjunction with tool-use in woodpecker finches (Tebbich and Bshary 2004), it now seems much more plausible that capacities such as high flexibility shared by the clade were co-opted for the specific woodpecker finch niche (Tebbich et al. 2010).

This conclusion is timely, coinciding with findings from a recent paper in which it was postulated that physical intelligence in corvids preceded the evolution of tool-use in New Caledonian crows and evolved in another context, possibly complex sociality (Bird and Emery 2009). In Darwin's finches, we consider it likely that certain cognitive characteristics such as high explorative tendency or flexibility in the stem species coupled with an untapped resource were the prerequisites for the development of tool-use. In contrast to Bird and Emery (2009), we are not implying that anything more cognitively sophisticated than

enhanced trial-and-error learning and/or exploration preceded tool-use in Darwin's finches. Indeed, the failure of Darwin's finches to transfer rule-learning to different versions of a physical task, even when very simple perceptual cues were available indicates that the basic cognitive abilities of Darwin's finches are at a lower level compared to corvids (reviewed in Emery and Clayton 2009). This study has contributed further evidence showing that tool-use, even that involving some degree of task-specific modification and selectivity (Teblich and Bshary 2004), must not necessarily be associated with sophisticated cognition, rather there are simpler cognitive routes which are capable of producing successful and seemingly complex tool-use.

## **ACKNOWLEDGMENTS**

We are grateful to Birgit Fessl for support in all facets of this study and to Roger Mundry for his detailed statistical advice. Caroline Raby, Viviana Morales, Mari Cruz Jaramillo, Tania Quisingo Chiza, Paola Buitron Lopez, and Eduardo Sandoval provided valuable field assistance and help with experiments. Patrick Meidl provided vital support in organizing vast amounts of data. Thanks to Eric Koch and Andy Burnley for constructing experimental apparatus, Theo Weber for graphics depicting the cane- and seesaw apparatus and finally to Henrik Brumm for valuable comments on the manuscript.



# **PHYSICAL COGNITION AND TOOL-USE: PERFORMANCE OF DARWIN'S FINCHES IN THE TWO- TRAP TUBE TASK**

Teschke I. and Tebbich S.  
(accepted) *Animal Cognition*

### **Abstract**

*The trap tube is a classic test of causal reasoning abilities in animals in the physical domain. Recently, a modified version of this task improved its diagnostic capacity and allowed testing of non-tool-using animals. We used this modified two-trap tube task to compare the cognition of two Darwin's finch species: the woodpecker finch (*Cactospiza pallida*) a tool-using species, and the small tree finch (*Camarhynchus parvulus*) a closely related non-tool-using species. Not all woodpecker finches use tools in nature, we therefore also tested non-tool-using individuals to assess the effect of experience on trap tube performance. No small tree finches and only two non-tool-using woodpecker finches solved the initial task which was operated using a pre-inserted piston. One tool-using woodpecker finch solved the task when allowed to use its own tool instead of the pre-inserted piston. The fact that none of these subjects transferred their knowledge when the features of the task changed, suggests that in this species, neither experience using tools nor the genetic composition of a tool-user are associated with the general physical cognitive skills required to solve the trap tube task.*

The trap tube task of Visalberghi and Limongelli (1994) has been one of the most prevalent assays of causal reasoning in solving a physical problem in animals. This task requires a subject to use a tool to extract a reward contained in a clear plastic tube without pushing it into a vertical trap located along the length of the tube. The central question has traditionally been the cognitive level of the strategy employed in solving the task, i.e. did the successful animal solve this task by abstracting a generalized causal rule rooted in the physical principles of the task (gravity and/or surface continuity) or via a simple associative rule based on the observable features of the task, i.e. "push from the side that is furthest from the food"? To differentiate between these possibilities, the authors devised a control test for successful animals in which the tube is inverted 180 degrees, rendering the trap non-functional. If the subjects have learned about the function of the trap, they should immediately cease to respond to the position of the non-functional trap.

To date, primates, including capuchin monkeys (*Cebus paella*) chimpanzees (*Pan troglodytes*), orang-utans (*Pongo pygmaeus*), bonobos (*Pan paniscus*), and one gorilla

(*Gorilla gorilla*) (Limongelli et al. 1995; Martin-Ordas et al. 2008; Mulcahy and Call 2006; Povinelli 2000; Visalberghi and Limongelli 1994) and several bird species such as woodpecker finches (*Cactospiza pallida*), the New Caledonian crow (*Corvus moneduloides*) and three non-tool-using parrot species (Bluff et al. 2007; Liedtke et al. 2010; Tebbich and Bshary 2004) have been tested in this paradigm. The results of these tests have not provided any conclusive evidence that these species are capable of using anything more cognitively complex than simple procedural rules to solve the task (Bluff et al. 2007; Penn et al. 2008; Penn and Povinelli 2007; Visalberghi and Tomasello 1998).

## Limitations of the inverted control task and the two-trap tube

The finding that humans also continue to avoid the inverted trap highlighted major conceptual flaws of this task, for instance that there is no incentive to stop avoiding the trap in the control condition and that inverting the tube changes the task features so drastically that subjects might perceive it as a new task and therefore disregard the trap (Silva et al. 2005).

Seed et al. (2006) and Tebbich et al. (2007) responded by devising a modified tube task that featured two traps: a functional trap sealed with a black disc at the bottom and a non-functional trap, to preclude the use of some simple cues such as “pull away from the trap”. They also designed a new set of transfer tasks in which the arbitrary visual task features were systematically varied while the underlying causal task properties were conserved. Presumably, a solution to the sequence of all transfer tasks can only be attained through the extraction of more sophisticated and generalized rules such as the fact that unsupported objects always fall (the observable effect of gravity) and that objects cannot pass through barriers.

The new task could also be used to test non-tool-using animals: the tool was pre-inserted into the tube and the reward was located between two clear discs so that it would move in the direction that the stick is pulled or pushed. Seed et al. (2006) tested eight rooks (*Corvus frugeligus*) a non-tool-using corvid species, with this paradigm. Seven of the eight rooks solved the initial problem and also succeeded in the first transfer task. Only one was successful in the subsequent pair of transfer tasks, suggesting that it had formed a generalized rule to solve the task. However, in another trap tube study with rooks which included some of the novel transfer tasks used by Seed et al. (2006), only three of seven birds solved the initial problem and none solved the transfer task (Tebich et al. 2007).

New Caledonian crows (Taylor et al. 2009a; Taylor et al. 2009b), parrots (Liedtke et al. 2010) and chimpanzees (Seed et al. 2009) have also been tested in modified versions of the two-trap tube task. Three of six New Caledonian crows which solved the initial task and subsequent transfer tasks using their own tools, were successful on two transfer tasks but failed the third. This indicated that they did not have a full appreciation of the underlying physical problem though the fact that all crows solved the analogous trap table task indicates that they had possibly learned something more general about surface continuity. None of the parrots were able to solve the initial version of a single trap tube task with a pre-inserted tool

and though two of the parrots solved the two-trap tube task when able to move the reward directly with their beaks, the study does not allow determination of the rule they extracted to solve this task (Liedtke et al. 2010). Six chimpanzees were tested in a two-trap tube task that could be operated without using a tool, by inserting a finger into small holes in the tube wall. One individual solved the initial task and all three transfer tasks which “supports the notion that they had used some form of mental representation” to solve the problem (Seed et al. 2009). Moreover, the authors found a significant effect of tool inclusion and experience on success: those animals that did not have to use a tool and that had prior experience in a similar task were most successful.

## The link between tool-use and general physical intelligence

In humans, tool-use usually involves a generalized appreciation of the physical world in the causal terms of gravity, the functional relationship between an object and the tool used to manipulate it as well as understanding the functional properties of tools. On the surface, the tool-use of some animals also appears to be a remarkable feat, requiring sophisticated high-level cognitive strategies. The findings that tool-use correlates with increased brain size in primates (Reader and Laland 2002) and birds (Lefebvre et al. 2002), suggests that this behaviour is indeed cognitively demanding, possibly because its deployment requires complex information processing abilities. Reflecting this, much research on animal tool-use during the past two decades has focused on elucidating the cognitive level of information processing associated with this unusual behaviour in various tool-using species, mostly primates. In this study, we were specifically interested in testing the hypothesis that a tool-using species might have access to a greater appreciation of general physical interactions than a non-tool-using species, either by virtue of their genetic composition or through experience.

To this end, we compared the performance of tool-using woodpecker finches and the closely related non-tool-using small tree finches (*Camarhynchus parvulus*) in the two-trap tube paradigm with a pre-inserted tool. These are closely related species belonging to the Darwin’s finch clade which is endemic to the Galápagos archipelago. Woodpecker finches use cactus spines or twigs to extract arthropod larvae and adults from crevices and holes (Eibl-Eibesfeldt 1961). However, Tebbich et al. (Tebich et al. 2002) demonstrated that the propensity and ability to use tools is linked to the environment: in coastal areas where food is scarce and hard to access, all individuals are capable of using tools and do so frequently, whereas in humid areas at higher altitudes where food is abundant and easy to access, woodpecker finches hardly use tools and even the ability to use tools seems to vary.

In contrast to chimpanzees, the ability to use tools in woodpecker finches is not dependent on social learning, rather they have a specific genetic predisposition to acquire tool-use in a sensitive learning period early in ontogeny through a process which involves trial-and-error learning (Tebich et al. 2001). The evidence comes from the fact that juvenile, hand-raised woodpecker finches from humid areas learned to use tools regardless of whether they had a

tool-using tutor or a tool-using parent whereas adult individuals from the same area seemed to be unable to use tools in captivity and also failed to learn the technique from a conspecific tutor.

Woodpecker finches are selective in the tools they use and can modify them to suit a task at hand (Tebbich and Bshary 2004). Moreover, one woodpecker finch successfully solved the inverted control task of the single trap tube task whereas the other five tested failed, but careful analysis revealed that the successful bird seems to have observed the effect of tool manipulation on the movement of the reward. Thus, another goal of this study was to re-evaluate the performance of woodpecker finches with the new two-trap tube paradigm.

We predicted that if tool-use was associated with enhanced general physical cognition in woodpecker finches, then they should outperform small tree finches in the trap tube task. However, if generalized physical intelligence evolved in a different context, small tree finches should match or even exceed their performance.

The fact that not all woodpecker finch individuals use tools (Tebbich et al. 2001; Tebbich et al. 2002) provided an opportunity to assess the effect of tool-using experience on general physical cognition: experience with tools improves performance in at least some physical tasks involving the use of tools (Hauser et al. 2002). Thus, we also compared the performance of tool-using and non-tool-using woodpecker finches in the two-trap tube with a pre-inserted tool. Our modified prediction was that if only experience with tools (and not the genetics of a tool-user) leads to a sophisticated appreciation of physical interactions, only the tool-using woodpecker finches should outperform small tree finches but not non-tool-using woodpecker finches.

It has been shown that task presentation has a strong effect on performance (e.g. Mulcahy and Call 2006; Seed et al. 2009). These studies highlight the fact that the physical problem itself is only one source of difficulty. The other major challenge is dealing with the intermediate manipulation of an object in order to move the food reward.

To compare non-tool-using animal's performance in the two-trap tube with that of tool-users, in several studies non-tool-users were trained to pull a pre-inserted stick that moved the food in order to allow them to operate the trap tube apparatus. This behaviour still falls within widely used definitions of tool-use (e.g. Beck 1980; van Lawick-Goodall 1970) but might not be considered tool-use according to others (see discussions in Bentley-Condit and Smith 2009; St Amant and Horton 2008). In any case, it is possible that this passive use of tools alters the cognitive load necessary to solve the task. It could well be that manipulation of a freely manipulable tool is a greater challenge than the pulling of the pre-inserted tool. However, it might also be that when allowed to use their own tools, tool-using woodpecker finches are able to grasp the physical interactions better because the problem is posed in a more natural context.

In our third experiment, we therefore allowed four additional tool-using woodpecker finches to use a freely manipulable straight stick tool—similar to their natural tools—to retrieve the reward rather than the pre-inserted stick. Comparison of these tool-using wood-

pecker finches with tool-using woodpecker finches that used the pre-inserted tool allowed a comparison of the cognitive load imposed by the two different methods of operating the task.

## GENERAL METHODS

### Study area, subjects and housing

The study was carried out at the Charles Darwin Research Station on Santa Cruz Island in the Galápagos Archipelago, Ecuador from October 2007 - March 2008 and September 2008 - January 2009. Some test subjects participated in other experiments testing physical cognition, before or after the trap tube experiments described here. A summary clarifying the order of experiments and the participation of each bird in each experiment is given as electronic supplementary material. Appendix 1 (Table A1) of the electronic supplementary material details the history of the birds and their experience in other experiments which required them to use a tool. A total of 18 woodpecker finches and 9 small tree finches were mist-netted for this study.

Following capture, finches were first kept in a small habituation cage (0.5 x 0.5 x 1m) for  $\leq 5$  days. Thereafter, the birds were maintained in outdoor aviaries (3.9 x 2 x 3m or 2 x 1 x 2m) where they were kept singly and visually isolated from each other on a diet of mashed hard-boiled egg, grated carrot, mixed with commercial bird food mix (Orlux®). Additionally, the birds received fresh fruit and fresh moths daily following testing. Subjects were kept at 100% of their free-feeding weight. Aviaries were furnished with natural branches and an experiment table on which the apparatus were presented.

### Assessment of tool-using ability of woodpecker finches

Tool-using ability of woodpecker finches was always assessed prior to participation in experiments. For this purpose, we drilled holes into natural logs (logs about 50mm long x 120mm wide; holes 40mm deep x 10mm wide) and baited the holes with the preferred rewards of the subjects. Birds were observed in sessions of 20-30 minutes in which a baited log was placed in a subject's aviary along with abundant tools and tool material and we observed to see whether the subject used tools to retrieve the food reward (see Appendix 2, Section 1.2 for details). An individual was categorized as a non-tool-user if it did not show successful tool-use within 530 min (ca. 9 hours) of accumulated observation. All tool-users were observed to use tools within the first 90 min. of observation but on average within the first 28 min.

The categorization of tool-users vs. non-tool-users based on this method was substantiated by the fact that those six woodpecker finches that were held in long-term captivity and had been classified as non-tool-users by the method detailed above, were never seen to use tools in  $>1$  year duration in captivity. Furthermore, our findings that only two of eight

woodpecker finches captured in the humid zone were observed to use tools, while all Arid zone birds were found to use tools reflects the frequency of natural occurrence of tool-use in woodpecker finches. In the humid zone, Tebbich et al. (2002) observed only six instances of tool-use during 430 minutes of continuous focal observations in contrast to 134 instances of tool-use observed during 845 minutes in the Arid zone near the coast. In this habitat, 20 of the 21 individually identified subjects used tools.

## General experimental procedure

Experiments were conducted in the home aviaries of the birds and food was removed from their aviaries 2 hours preceding testing. Rewards were the preferred food of each individual (generally mealworms or moths). Apparatus were always baited out of sight of the subject and for each trial, placed onto the experiment table within the home aviary. The experimenter then left the room and observed the trial via a camcorder (JVC GZ-MG130EK hard disk camcorder). All experiments were recorded with the camcorder.

## Training

Prior to beginning experiments, all subjects were trained to pull a stick protruding from a transparent Perspex® tube (175mm long x 20mm wide) that was open only at one end and was fixed to a wooden block (300mm x 120mm). In this training phase, the side to which the open tube end pointed was randomized and counterbalanced. A stick with two discs near the end and food between them was inserted into the tube and the subject could rake the food reward out of the tube by pulling the stick. Subjects had to retrieve the food in 6 consecutive trials before advancing to test trials.

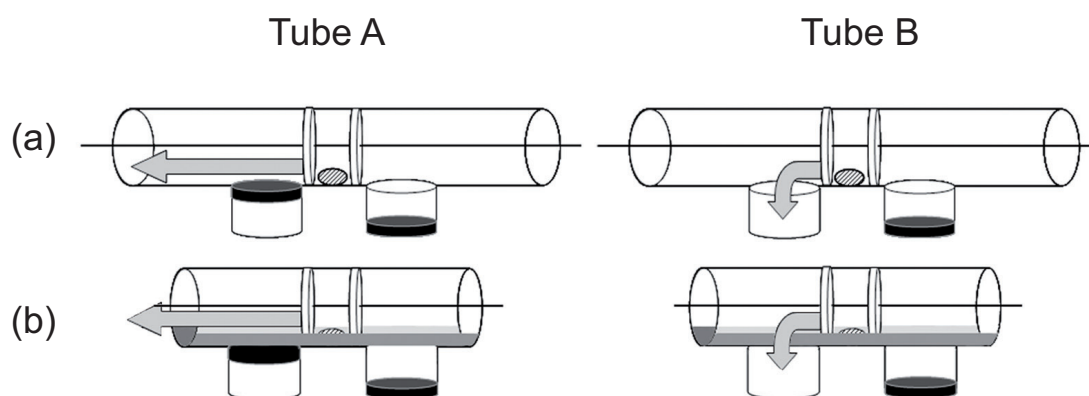
## Ethical Note

Permission to catch the birds and to conduct the study was given by the Galápagos National Park. Eight of the woodpecker finches were held in long-term captivity ( $\geq 1$  year) for breeding purposes related to conservation (Appendix 4, Table A4). All other birds were held for the minimum amount of time required to complete the experiments, and then released at their site of capture following conclusion of our experiments.

## EXPERIMENT 1: TWO-TRAP TUBE

### Methods

**Subjects** Subjects were six tool-using woodpecker finches, eight non-tool-using woodpecker finches and five small tree finches. One small tree finch only completed 50 trials due



**Figure 2.1** (a) Trap tubes used in Experiment 1 and (b) those used in Experiments 2 and 3. For both experiments, Tube A is on the left while Tube B is on the right. In Experiment 3, the stick was not pre-inserted into the tube, rather, two sticks were placed in front of the apparatus. Arrows indicate the path of the reward for a correct response.

to illness and is therefore not included in the results. All birds were tested in this task during the first field season.

**Apparatus** The two-trap tube apparatus consisted of a horizontal, transparent tube (165mm long x 20mm wide) with two traps: a functional one with a black disc sealing the bottom and a non-functional trap with either a black disc sealing the top and flush with the inner hollow of the tube (Tube A, Figure 2.1a) or open at the bottom with no disc at all (Tube B, Figure 2.1a). These were the same initial testing conditions used by Seed et al. (2006). The tubes were held up at each end by a vertical, transparent Perspex® panel (140mm high x 120mm wide). These were inserted 120mm apart into a wooden base (300mm long x 120mm wide x 25mm high). The tubes were mounted approximately 65mm above the wooden base.

Half of the birds of each test group received Tube A while the other half always received Tube B. Each trap was mounted 25mm laterally from the centre. Two discs were attached to the pre-inserted piston as in the training trials and the reward was always placed centrally within the tube between the discs and could thus be moved by pulling the piston from either side. The ends of the piston protruded 20mm from each tube end.

## Experimental procedure

At the start of each trial, a reward was placed centrally within the tube and between the discs of the pre-inserted tool. The baited apparatus was then placed on the experiment table in the subject's aviary and the subject was given 5 minutes to either pull the stick so that the food fell into the trap and was lost or until it successfully extracted the food. Subjects were allowed to switch pulling sides during a trial. We scored whether they were successful or not in attaining the food.

Birds were tested in blocks of 10 trials, receiving one to two blocks per day on 5 to 7 consecutive days per week. If the subject did not approach the apparatus or make a decision within 5 minutes, a habituation trial was conducted in which the bird was required to take a reward which was placed centrally on top of the apparatus before the trial was repeated. If the bird needed more than 3 habituation trials in one block, the block was ended prematurely.

**Success criterion** Birds were given between 140 and 180 trials to meet the success criterion: a bird had to make 15 or more correct choices within two consecutive blocks of 10 trials to meet the success criterion. Specifically, the number of correct responses in one of the two blocks had to be at least 7 consecutively correct and in the other at least 8, or in one block all 10 correct. This criterion was derived using a Monte Carlo simulation which is more reliable than simple binomial statistics because it reduces the likelihood of type-I errors (details in Tebbich et al. 2007).

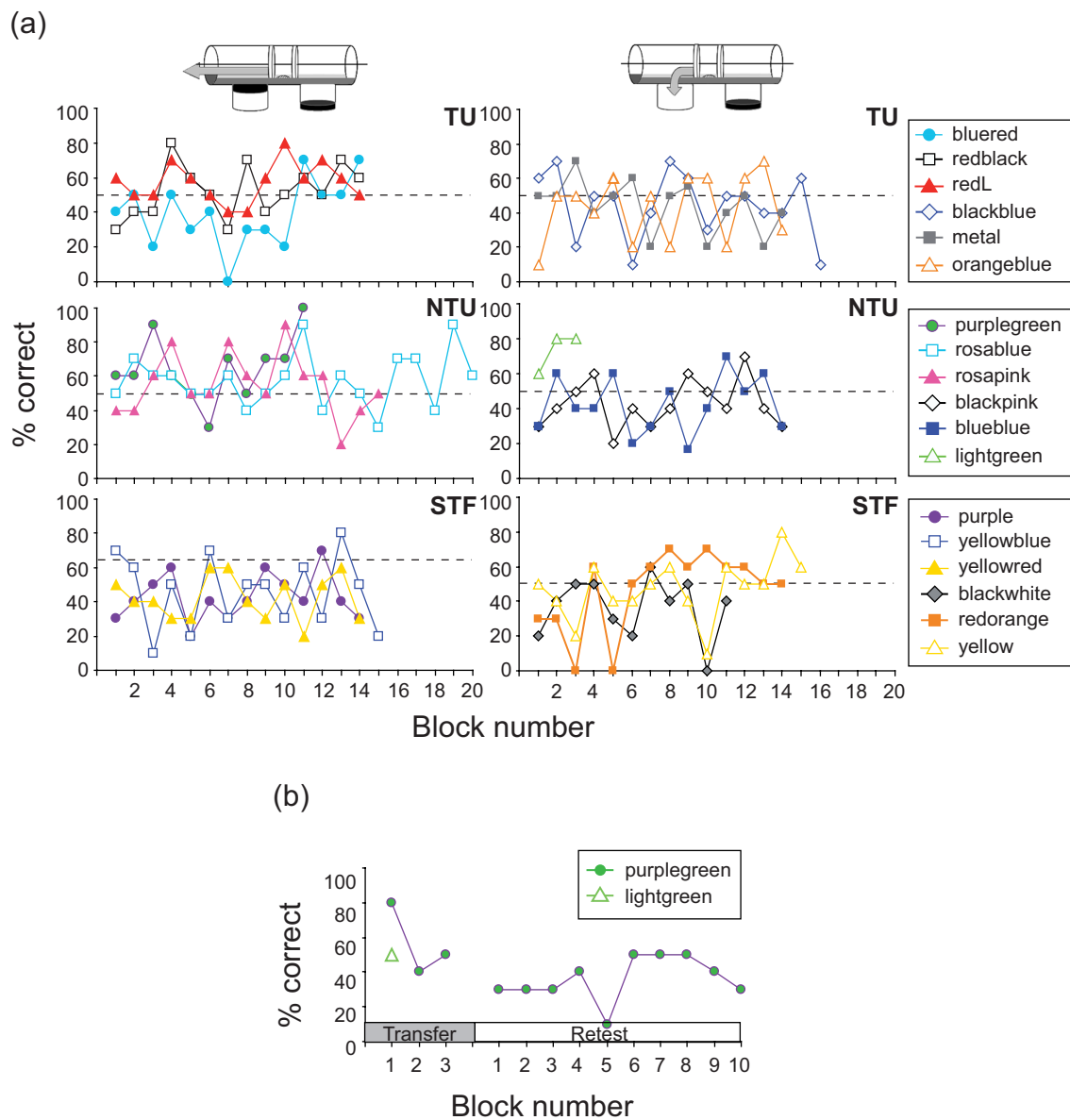
The orientation of the apparatus changed trial by trial so that the correct side was always on the right side on half of the trials and on the left side on half the trials according to a randomized, balanced schedule.

A bird that met the success criterion in its initial task was then given no more than 20 trials to solve the transfer task, which was simply the version of the tube that it had not seen before.

**Side bias correction** Animals often develop strong side biases in two-choice tests, since only choosing one side results in a 50% success rate. It is therefore standard practice in experimental psychology to apply a correction procedure to prevent the animals from using such a strategy. Thus in our experiments, when a bird made 6 consecutive choices on one side, we only presented the reward on the non-preferred side in subsequent trials until the bird chose this side once. At this point, we reverted to the regular, randomized and balanced schedule.

## Results and Discussion

None of the birds were able to solve the initial version of the task and therefore no birds were tested in the transfer task. Table A4 (Appendix 4) contains the exact number of trials given to each bird. We speculated that the failure to solve the initial task might be attributed to two features of the apparatus. First, the tube might have been too long for the birds to learn about the contiguity between their pulling the stick and moving the reward and possibly they were not able to transfer this knowledge from the training sessions in which they learned how to operate the stick and the apparatus due to the perceptual differences between the apparatus used in training and testing. Second, it is possible that the transparency of the apparatus made it difficult for the birds to discern the relevant features of the apparatus, particularly the trap. Therefore, for the next experiment, we modified the tube to deal with these points as described in the next section.



**Figure 2.2** (a) Performance of all birds in Experiment 2 as percent of trials correct per block. Birds initially tested with Tube A are plotted on the left column while those originally tested with Tube B are plotted on the right. The horizontal dotted line represents chance performance (50% of trials correct). Top row: tool-using woodpecker finches (TU); middle: non-tool-using woodpecker finches (NTU); bottom: small tree finches (STF). (b) Transfer performance of two non-tool-using woodpecker finches and the retesting of purplegreen with its original trap tube (Tube A).

## EXPERIMENT 2: MODIFIED TWO-TRAP TUBE

### Methods

**Subjects** This experiment was conducted over both field seasons. We tested six small tree finches, 6 non-tool-using and six tool-using woodpecker finches in this experiment. All woodpecker finches had been tested in Experiment 1, having received between 140 and 180 trials, while two of the small tree finches had already received 140 trials each in the previous experiment (Appendix 4, Table A4). Subjects were given between 139 and 200 trials to meet the success criterion on the initial task and up to 30 trials to solve the transfer task. As in Experiment 1, the transfer task was simply the tube that a successful bird had not seen before. The success criterion and experimental procedure was the same as for the previous task and the two tube conditions (Figure 2.1b) were the same as in the last experiment.

**Apparatus** The tubes from the last experiment were modified to make the task easier to solve: the tubes were shortened (105mm long) and the lower half of the tubes was painted dark grey to accentuate the features of the task. Furthermore, the Perspex® supporting panels were trimmed (85mm high x 55mm wide) and moved closer to one another (80mm apart), thereby lowering the tube slightly (45mm above wooden base). A wider wooden base into which the supports were inserted, was constructed (200mm wide x 300mm long). The piston was shortened and still protruded 20mm from each end of the tube. Subjects who had been trained and tested in Experiment 1 were not given further training prior to this experiment unless more than 2 weeks had elapsed between the experiments. In this case, we checked to make sure the subject recalled how to operate the apparatus by testing them briefly with the training apparatus.

### Results and Discussion

Only two non-tool-using woodpecker finches (purplegreen and lightgreen) solved the initial task (Figure 2.2a, middle row) while none of the tool-using woodpecker finches or small tree finches were successful. There was no significant difference in the proportional number of successful individuals when tool-using and non-tool-using woodpecker finches were compared (Fisher's exact test:  $p = 0.455$ ) nor was there a difference in the proportional success between pooled tool-using and non-tool-using woodpecker finches and small tree finches (Fisher's exact test:  $p = 0.529$ ). However, both of the birds that solved the initial task immediately failed the following transfer task (Figure 2.2b), indicating that they had solved the task using simple rules based on the arbitrary visual features of the task such as "pull towards from the upper black disc".

The interpretation is more complicated in the case of purplegreen. This bird responded correctly in 8/10 trials in its first block of the transfer test with the new tube (the first 6 consecutive transfer trials were correct), but made only 5/10 correct responses in each of the follow-

ing two blocks. This was surprising, given that the bird started out so well. To see whether this failure might have been due to a lack of motivation, we re-tested it with its original tube. In the next 100 trials with its original task, it never reached criterion (Figure 2.2b). This inability to form a stable procedural rule over time could be due to a lack of motivation, though based on the quick approach of all birds to the apparatus in most trials, this does not seem likely. Another possibility is that reverting between tubes confused the subject and affected its memory about what it had previously learned. Finally, it is also conceivable that the bird simply reached the criterion by chance. Liedtke et al. (2010) also observed that some birds reached criterion early on and then performed unreliably in subsequent trials.

The success of the two non-tool-using woodpecker finches in the initial task of Experiment 2 might be attributed to their longer period in captivity preceding Experiment 2 than small tree finches and tool-using members of the same species. On average, non-tool-using woodpecker finches began this experiment 242 days after being caught while tool-using woodpecker finches and small tree finches began it 60 and 53 days respectively after being caught. The two successful non-tool-using woodpecker finches began testing 115 and 74 days respectively, after being caught.

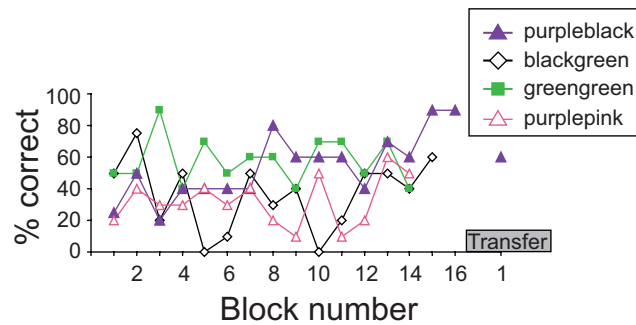
An alternative explanation for the fact that woodpecker finches were able to learn something specific about the task and not small tree finches is that all woodpecker finches tested in Experiment 2 had previously been exposed to at least 140 trials of Experiment 1, whereas 4/6 small tree finches had never been tested with a trap tube at the beginning of this experiment. Thus, some small tree finches might also have solved the initial task if they had previously had exposure to Experiment 1. An effect of experience has been reported for chimpanzees: chimpanzees with prior experience in a two-trap problem were more successful in a new variation of this problem than inexperienced individuals (Seed et al. 2009).

## **EXPERIMENT 3: MODIFIED TWO-TRAP TUBE WITHOUT PRE-INSERTED TOOL**

### **Methods**

**Subjects** Four tool-using woodpecker finches were tested in this experiment, all during the second season.

**Apparatus** We used the same apparatus and procedure as in Experiment 2 (Figure 2.1b), with the exception that the pre-inserted tool was not available. Instead, we always provided two sticks (80mm long) in front of and central to the apparatus which the birds had to insert and manoeuvre themselves in order to extract the food reward in each trial. We provided two sticks because the birds would sometimes lose a stick during the trial and we scored success as well as number of inserts and switches between sides.



**Figure 2.3** Performance of all birds in experiment 3 as percent trials correct per block. Transfer performance for purpleblack is shown on the far right. The dotted line signifies chance performance (50%).

## Results and Discussion

Only one individual (purpleblack) solved the initial version of this task (Figure 2.3), but it immediately failed in the subsequent transfer task. This implies that purpleblack had used arbitrary features of the task to solve the initial problem. Furthermore, in contrast to the successful woodpecker finch “rosa” of Tebbich and Bshary (2004), we did not find a difference in the number of tool insertions in the first 20 trials (median insertions = 1, range = 1-3) and last 20 trials (median insertions = 1, range = 1-5) for purpleblack (Wilcoxon signed-ranks test:  $z = -1.536$ ,  $p = 0.125$ ), which would have suggested the implementation of the trial-and-error strategy “monitor the effect of the tool on the reward”. Thus, it seems that purpleblack solved the initial task by picking an arbitrary cue to guide its choice, such as “pull towards the upper black disc”. In the transfer task (Tube B), the cue was not available or at least altered in a way which might have confused the subject.

The fact that there was not a significant difference in the number of tool-using woodpecker finches to solve the initial task with the pre-inserted tool (Experiment 2) and with a freely manipulable tool (Fisher’s exact test:  $p = 0.455$ ) does not support the hypothesis that the cognitive load imposed in the two different task operation methods differed. However, due to the small sample size this negative result needs to be interpreted with caution.

## GENERAL DISCUSSION

In this study, we assessed the general physical problem-solving abilities of two closely related Darwin’s finch species: the small tree finch and the woodpecker finch using the two-trap tube task with a pre-inserted tool that could be operated by both species. Furthermore, we assessed the effect of tool-using experience on general physical cognitive abilities in woodpecker finches and controlled for the effect of the unknown cognitive load imposed by the operation of a freely manipulable stick tool and a pre-inserted raking tool.

The comparison of woodpecker finches and small tree finches in Experiment 2 did not provide evidence that woodpecker finches excel at solving the two-trap tube task and by extension that they have a more sophisticated understanding of physical interactions involved in the task. Though only woodpecker finches solved the initial task, all failed in the following transfer task. Furthermore, the proportion of successful woodpecker finches in the initial task was not significantly higher than for small tree finches.

The fact that small tree finches performed equally well or better than woodpecker finches in other tasks testing physical cognition (Chapter 1) provides further reason to be cautious in interpreting the poor performance of the small tree finches in the trap tube tasks.

The results parallel the findings of the previous woodpecker finch study (Tebbich and Bshary 2004) in the sense that woodpecker finches learned to avoid a trap but did not seem able to appreciate the function of a trap even after being given numerous opportunities to do so. We also did not observe that tool-experienced woodpecker finches performed better in the trap tube with the pre-inserted stick (Experiment 2). Indeed, the only woodpecker finches that were able to solve the first stage of this task were non-tool-users.

One tool-using woodpecker finch solved the initial task when allowed to insert a stick tool (Experiment 3) but none were able to do so using the pre-inserted tool (Experiments 1 and 2). This might be due to the more natural context of task presentation in Experiment 3—even chimpanzees and orangutans perform better in the original trap tube task when allowed to apply a “species-specific tool-using action” (Mulcahy and Call 2006, p. 194). However, the failure of this subject in the transfer task indicates that it also probably solved the initial task using an arbitrary cue that was altered in the transfer condition.

When one considers the relative uniformity in the natural tool-use of woodpecker finches whereby tools are used only in one context and in one way, it makes sense deploying tools in this species does not necessitate generalization of physical interactions—simple situation-specific rules probably suffice to get the job done. However, the low number of individuals that were able to solve the initial task even using simple context-specific rules, shows that an easier task would be needed to detect a significant species difference with such a low sample size. One possibility would be to present them with a task which allows direct movement of the food with the beak as in Liedtke et al. (2010).

The fact that large-brained rooks are able to extract generalized rules in a task where small tree finches do not even succeed in successfully applying a simple procedural rule in first stage of the task suggests a qualitative difference in the cognition of these non-tool-using species. Likewise, the comparison of the performance of tool-using woodpecker finches and New Caledonian crows in the two-trap tube task that was operated with a freely manipulable tool also shows that larger brained New Caledonian crows have a higher propensity to form a general rule while woodpecker finches only can form a situation-specific rule. Finally, one chimpanzee that was tested in a further variation of the two-trap tube paradigm was able to solve a series of transfer tasks that had no simple perceptual cue in common. The summary of these results suggests that large brain size might be a better predictor of the ability to form

a generalized rule pertaining to the physical properties of the task than tool-use. Only the performance of parrots does not fit in with this interpretation. Parrots are relatively large-brained but they failed to even extract a simple procedural rule to solve the initial single trap tube task with a pre-inserted tool when given between 100 and 200 trials to do so. Even woodpecker finches with their presumably smaller proportional brain sizes solved the initial task using a simple rule (see Liedtke et al. 2010 for a detailed discussion).

Woodpecker finch tool-use is characterized by selectivity, modification, and high frequency in natural populations and furthermore “is not a stereotypic behavioural pattern, but is open to modification by learning” (Tebbich and Bshary 2004, p. 696). Nevertheless, all studies to date which have investigated cognition related to tool-use in woodpecker finches have failed to provide any evidence that this species possesses sophisticated physical cognitive abilities, that they use mental representation and planning in problem-solving related to tool-use (Tebbich and Bshary 2004; Chapter 1) nor have they yielded evidence that woodpecker finches must learn this seemingly complex technique from other conspecifics (Tebbich et al. 2001). In woodpecker finches, simple cognitive solutions appear to suffice for the ontogenetic development of tool-use and for its deployment. In particular, trial-and-error learning appears vital to the species in acquiring tool-using skills in ontogeny (Tebbich et al. 2001) and also in solving a battery of physical problems.

## ACKNOWLEDGEMENTS

IT was supported by the German research foundation (DFG, Project Nr. TE628/1-1) and ST by the Austrian Science Fund (FWF, Project Nr. V95-B17). The experiments comply with the current laws of the country in which they were performed. We are thankful to the Charles Darwin Research Station for support and TAME for reduced ticket fares. We are also grateful to Dr. Birgit Fessl for support in all facets of this study. Caroline Raby, Viviana Morales, Mari Cruz Jaramillo, Tania Quisingo Chiza, Paola Buitron Lopez, and Eduardo Sandoval provided valuable field assistance and help with experiments. Patrick Meidl provided vital support in organizing vast amounts of data. Thanks to Andy Burnley for constructing experimental apparatus and to Sue-Anne Zollinger for helping to make the figure depicting the experimental apparatus.

## CHAPTER 3



# INVESTIGATING THE RELATIONSHIP BETWEEN FORAGING AND LEARNING ABILITIES IN TWO SPECIES OF DARWIN'S FINCHES

Tebbich, S., Stankewitz S. and Teschke, I.

(manuscript)

### Abstract

*The ability to unlearn a previously established association is an important component of behavioural flexibility and may vary according to species ecology. Previously, two closely related, sympatric Darwin's finches, the woodpecker finch (*Cactospiza pallida*) and the small tree finch (*Camarhynchus parvulus*), were found to differ significantly in their ability to solve a novel operant task and in reversal learning, a test of behavioural flexibility. Small tree finches outperformed woodpecker finches in reversal learning but performed worse in the operant task. We attributed this difference to the habit of woodpecker finches to engage in long bouts of energetic pecking at a substrate during extractive foraging. Persistently repeating one action without reward could favour performance in operant tasks but also limit behavioural flexibility. Here, we tested whether perseverance is the reason for woodpecker finches' depressed reversal learning performance. Two modified reversal conditions allowed the disentanglement of two sources of error in reversal learning: perseverant choice of the previously rewarded stimulus and failure to respond to the previously non-rewarded stimulus. Our prediction was that woodpecker finches should make more errors of perseverance than small tree finches. Since performance differences could also be influenced by reaction to novelty, we compared neophilic and neophobic responses in woodpecker finches and small tree finches and related them to reversal learning proficiency. We found no significant species difference in reversal learning under these new conditions, suggesting that the observed difference from the previous study is not attributable to high perseverance in woodpecker finches. However, woodpecker finches were less neophobic and there was some indication for a negative correlation between neophobia and reversal learning performance.*

Learning enables animals to fine-tune their behavioural response to their respective environment. Thus, learning abilities may vary with feeding ecology, even between closely related species (e.g. Garcia et al. 1974; Laverty and Plowright 1988; Ratcliffe et al. 2003) and between populations from different habitats (Roth et al. 2010). The complexity and the variability of an environment is thought to be one of the key factors that determine the optimal rate of learning (Godfrey-Smith 2001). Species or populations that live in complex or fluctuating environments must react more readily to changes and should therefore be more

flexible than individuals from stable environments (Day et al. 2003; Jones 2005; Robinson 1990; Shettleworth 1998; Tomasello and Call 1997). Even closely related species that live in the same habitat might experience the predictability of relevant resources differently depending on their foraging ecology. The ability to inhibit previously successful responses is one factor that could enhance flexibility under changing conditions and the most widespread paradigm utilized to test this aspect of flexibility is that of reversal learning. In reversal learning tests, subjects first must learn a simple discrimination and once a set learning criterion is reached, the reward contingencies are reversed in a second learning phase. A wide range of species have been tested in the serial reversal paradigm in an attempt to find a comparable measure of learning performance (Bittermann 1965; Davey 1989; Mackintosh and Holgate 1969; Mackintosh et al. 1968). More recently this experimental paradigm has been used to compare closely related species and different populations of one species to test more precise predictions about the relationship of behavioural flexibility and the complexity of the environment (Bond et al. 2007; Day et al. 1999; Roth et al. 2010).

However, differences in learning abilities can also be due to differences in reactions to novelty, which can either directly or indirectly influence learning. For instance a novel stimulus could evoke aversion or attraction during an interaction and thus influence learning performance directly. Seferta et al. (2001) discovered that feral pigeons (*Columba livia*), which are afraid of novel stimuli, are slower at learning an operant task than the less fearful Zenaida doves (*Zenaida aurita*). Furthermore, Webster and Lefebvre (2001) found the same pattern when comparing the relationship between problem-solving and fearful reactions towards novel stimuli in five different species of passeriformes and columbiformes and also between individuals. However, not only the aversion of novelty but also the attraction to novelty can influence learning. For instance Auersperg et al. (submitted) found that the exceptionally explorative Keas (*Nestor notabilis*) were faster at finding solutions to a problem-solving task with four possible solutions than the less explorative New Caledonian crows (*Corvus moneduloides*).

Aversion to novelty is thought to be driven by neophobia which is defined as avoidance of a food item, object or place only because it is novel, whereas the attraction to novelty is thought to be driven by neophilia, defined as the spontaneous attraction of an animal to a food item, object or place simply because it is novel (Thorpe 1956). Some theoretical models consider neophobia and neophilia as opposing ends of one behavioural continuum (Hogan 1965; Thorpe 1956) while others see them as two distinct, but related motivational systems which can be aroused simultaneously (Chance and Meade 1955; Greenberg and Mettke-Hofmann 2001; Hughes 1997; Montgomery 1955; Russell 1973). Most importantly it is believed that the two motivational systems are driven by different selective forces and may therefore vary independently of each other, depending on species ecology. While it is surmised that neophobia is driven by the costs of exploration, such as predation, neophilia is thought to be driven by the benefits of exploration such as the discovery of novel resources (Greenberg and Mettke-Hofmann 2001).

In the current study, our goal was to test predictions about the relationship between extractive foraging, and reversal learning and reaction to novelty in two species of Darwin's Finches, the woodpecker finch (*Cactospiza pallida*) and the small tree finch (*Camarhynchus parvulus*). A previous study showed that these two closely related species differ significantly in reversal learning and in learning an operant task (Chapter 1): small tree finches outperformed woodpecker finches in a classical colour discrimination reversal paradigm (Chapter 1, Experiment 1) whereas woodpecker finches outperformed small tree finches in a novel operant task (Chapter 1, Experiment 4). We attributed these findings to the different feeding ecologies of the species, especially to the persistent foraging style of woodpecker finches. The sympatric woodpecker finch and the small tree finch have a similar diet composition and also utilize similar feeding techniques (Tebbich et al. 2004) but show a pronounced difference in their proportion of extractive foraging. In contrast to small tree finches, woodpecker finches often engage in long bouts of energetic pecking at wood and probing into crevices without immediately obtaining their prey. This foraging strategy requires high levels of perseverance, and this, in turn, requires that a subject continues with an activity, even when it is not rewarded.

This dissimilarity in feeding ecology could be crucial in understanding the disparity in the performance of woodpecker finches and small tree finches in the learning experiments. On one hand, high perseverance can lead to success in an operant task, because frequent confrontation with an object increases the probability of accidentally making the movements required to solve the task. On the other hand, fast reversal learning requires just the opposite: an animal must be sensitive to not being rewarded for a previously profitable behaviour and respond by changing its behaviour. Extractive foraging that requires perseverance may therefore come at a cost, namely it might impede learning flexibility because high perseverance is likely to be associated with a low sensitivity to absence of reinforcement (Tebbich et al. 2010; Chapter 1). If this is the case, we could expect a disparity in flexibility between extractive and non-extractive foragers that is widespread among different taxa. An effect of extractive foraging on cognitive abilities has been demonstrated in a comparison between predominantly gum feeding marmosets (*Callithrix jacchus*) and more insectivorous tamarins (*Saguinus oedipus*): in a self-control paradigm the marmosets waited significantly longer for food than tamarins, which indicates that the patience needed to feed on gums may have selected for a more general ability to cope with delayed gratification (Stevens et al. 2005). Extractive foraging does not only seem to influence cognitive abilities but also reaction to novelty. In a comparative study of parrots Mettke-Hofmann et al. (2002) found that the duration of exploration correlated positively with the proportion of nuts in the diet. In contrast, extractive foraging correlated negatively the propensity to approach novel objects in Darwin's finches (Tebbich et al. 2009).

In the current study we aimed to test whether the difference in reversal learning found between the two species in Chapter 1 is indeed a consequence of a difference in sensitivity to a change in reward contingency (sensitivity to the absence of reinforcement) utilizing two

modifications of the classical reversal learning paradigm.

Following Tait and Brown (2007), we applied a reversal design that allowed the disentanglement of two possible sources of error in classical reversal learning which cannot be distinguished in the classical paradigm: in the “Perseverance” reversal (hereafter P reversal condition), the formerly rewarded colour ceases to be rewarded and a newly introduced colour becomes the rewarded stimulus while in the “Learned Non-Reward” reversal (hereafter LNR reversal condition), the formerly unrewarded colour is now rewarded and a newly introduced colour becomes the unrewarded stimulus (Figure 3.1).

In light of their extractive foraging style, we expected woodpecker finches to be less sensitive to a change in which a formerly rewarded stimulus is not rewarded anymore. If this is the reason for the poor performance of woodpecker finches, they should make more errors in the P reversal than in the LNR reversal and also make more errors in the P reversal than small tree finches.

As learning can also be influenced by reaction to novelty, another objective was to investigate whether small tree finches and woodpecker finches differ in their novelty responses, whether individual reaction to novelty was consistent across trials and how learning and reaction to novelty are related. A consistent inter-individual reaction to novelty indicates that this trait may be related to an individual's coping styles. If this is so, differences in reaction to novelty may not only directly influence reversal learning via attraction or aversion to novel stimuli but also indirectly via the coping style since studies on animal personality indicate that an animal's reaction to novel stimuli is likely to be correlated to the learning abilities of the species. For instance, Drent and Marchetti (1999) and Verbeek et al. (1994) found that in great tits (*Parus major*), slow explorers changed a previously established foraging habit more quickly than fast explorers, indicating that responses to novelty and reversal learning (i. e. learning of changed reward contingencies in a discrimination task) are co-varying traits within this species.

The mechanism underlying the relationship between reversal learning and reaction to novelty is not known. Verbeek et al. (1994) and Drent and Marchetti (1999) argue that fast explorers were quicker to establish a foraging habit, but slower at changing an established habit, whereas slow explorers quickly extended their search to other places when they did not find food readily at established sites. These are, however, two different (but not mutually exclusive) explanations that are related to the previously described components of reversal learning namely perseverance in choosing the previously rewarded stimulus and difficulty in learning that a previously non-rewarded stimulus is now rewarded. The data from the LNR and P reversal conditions in combination with the data on novelty reactions allowed us to test whether more neophobic birds are more flexible because they abandon a learned feeding habit more quickly (P reversal, learn that the previously rewarded stimulus is not rewarded anymore) or because they learn to choose a previously unrewarded stimulus more quickly (i.e. “remain alert to stimuli in the known environment” Verbeek et al. 1994, p. 119). To assess potential species differences in novelty reactions we compared neophilic and neophobic

responses towards novel objects in woodpecker finches and small tree finches and examined the relationship of these results with those of the learning experiments.

## METHODS

### Study area, subjects and housing

**Study area** This study was conducted on Santa Cruz, which is one of the larger, central islands (986 km<sup>2</sup>) of the Galápagos archipelago. Birds for the experiments were caught in the so-called Scalesia zone, located at an elevation of between 300m and 650m. This vegetation zone is characterized by the eponymous tree *Scalesia pedunculata* of the Asteraceae family which forms an evergreen, lush, moist forest. The branches and trunks of these trees are densely covered with epiphytic moss, lichens, ferns and bromeliads. Prey arthropods are abundant throughout the year in this area and can be found primarily in moss, on leaves and under bark (Tebbich et al. 2002).

**Study species** The study species were two closely related species of Darwin's Finches: the woodpecker finch and the small tree finch. They occur sympatrically in the Scalesia zone on Santa Cruz Island. Both species are members of the tree finch clade and within this group are members of a guild of mainly insectivorous tree foragers.

Woodpecker finches (~20g) have an elongated but powerful beak that is suitable for probing moss patches and pecking into wood and under bark to gain access to their prey. This species uses twigs or cactus spines held in their beaks as tools to probe under bark and in tree holes but shows this behaviour mainly in dry areas near the coast. Both species have a diverse food spectrum with a similar diversity of food types and foraging substrates (Tebbich et al. 2004). Woodpecker finches mainly feed on larvae of Hymenoptera and Coleoptera, but also in high amounts on adult insects and caterpillars. A smaller percentage of their diet consists of fruit, nectar and spiders. The main foraging techniques and substrates that woodpecker finches use are pecking on wood, probing into moss and chipping off bark from dead wood (Tebbich et al. 2004). Fruit, as well as green leaves and dead leaves that are still attached to the tree play a minor role as feeding substrates. In the Scalesia zone woodpecker finches hardly ever use tools. They perform this foraging technique mainly in the arid regions near the coast.

Small tree finches (~13g) have grasping beaks with convex curvature of both culmen (upper mandible) and gonys (lower mandible). They also rely heavily on insects as a food source, but depend more than woodpecker finches on fruit and nectar and additionally, they feed on seeds. These birds mainly glean prey off the surface of leaves attached to a tree but also forage to a lesser extent in moss and under bark (Tebbich et al. 2004).

The main difference in the feeding ecology of both species lies in the proportion of extractive foraging: woodpecker finches spent between 85-100% of their foraging time with extractive foraging techniques (e.g. pecking at bark, probing into moss) and whereas small

tree finches generally spent less than half of their foraging time with extractive foraging techniques (Tebbich et al. 2004).

**Catching and housing** These experiments were conducted in aviaries at the Charles Darwin Research Station on Santa Cruz Island. Ten woodpecker finches and 16 small tree finches were mist-netted and held in individual habituation aviaries (0.5 x 0.5 x 1.0m) during their first three to five days post-capture, until they were familiar with feeding and drinking from the provided dishes. The birds were then transferred to bigger outdoor aviaries (2.0 x 1.0 x 2.0m) where they were kept singly and visually separated from each other. The aviaries were enriched with natural twigs, branches and trunks and equipped with a concrete experiment table, a water bowl for drinking and bathing and a feeding dish. The birds were kept at 100% of their free-feeding weight on a diet of hard-boiled eggs, grated carrots, pieces of fruit and a prefabricated mix of dried insects (Orlux®) and fresh insects.

**Ethical note** The Charles Darwin Research Station and the Galápagos National Park provided the required permits to catch the birds and conduct these experiments. (Project PC-16-07, Permit Nr. PR.PT.P004.R02).

## Experimental procedures

### *General procedure*

Data were collected from October 2007 to March 2008 and from September 2008 to January 2009. Eight of the woodpecker finches were held in long-term captivity ( $\geq 1$  year) for breeding purposes related to conservation. All other birds were held for the minimum amount of time required to complete the experiments, and then released at their site of capture following conclusion of our experiments. Not all birds participated in all experiments (Table A1 of Appendix 1 contains details of experimental history).

Testing started between 11-72 days after release into the aviaries. The 8 woodpecker finches that were held in long-term captivity received the new reversal conditions (LNR and P) of this study 11-12 months after their introduction into captivity. Between the tests of novelty reactions and the learning experiments of this study, some birds were tested in a novel operant task, the classical reversal experiment mentioned in the introduction, and a number of other physical learning tasks (Chapter 1, Chapter 2, Tebbich et al. 2010, summarized in Table A1, Appendix 1). Birds were food-deprived two hours before each experiment with the exception of the neophilia experiment.

All tests were conducted in the bird's home aviaries with the experimental setup placed on the concrete table (0.5 x 0.2 x 0.8m). A perch was always affixed 30cm above the table surface to enable the bird to approach the task and inspect it from above while keeping some distance. Food rewards used in the experiments varied depending on individual preferences and included half a mealworm, a piece of moth, or, in the neophobia experiments, the normal

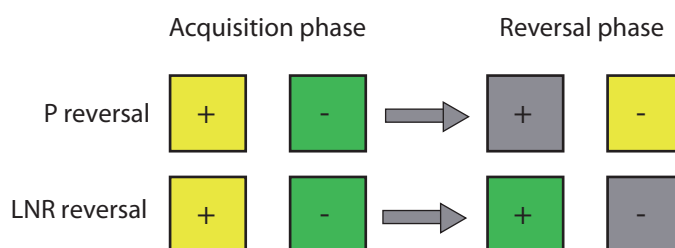
food mixture.

The experimental routine was as follows: the experimenter baited the apparatus out of sight of the bird in an observation room which was adjacent to each aviary and visually separated from the bird by a cloth screen. The experimenter then entered the aviary, put the apparatus on the experiment table, left the aviary, and observed the experiment from the observation room, either through a peep hole in the screen (neophobia experiments) or via a camcorder (JVC GZ-MG130EK hard disk camcorder) which was placed in front of the hole.

### ***Reversal learning: learned non-reward and perseverance conditions***

The classical reversal task poses two problems at the same time, namely learning that a formerly rewarded stimulus has ceased to be rewarded and that a formerly unrewarded stimulus is now rewarded but cannot determine which of these is the source of error in reversal learning (Gauntlett-Gilbert et al. 1999; Tait and Brown 2007). Tait and Browne's (2007) LNR and P reversal regimes (Figure 3.1) allowed us to differentiate between errors due to a persistent choice of the previously rewarded stimulus (P reversal) and errors due to failure to learn that the previously non-rewarded stimulus is now rewarded (LNR reversal).

The P and LNR reversal conditions both began with an acquisition phase in which subjects learned to discriminate between two different-coloured stimuli of which only one was reinforced with a food reward. After reaching the learning criterion (see below) it moved on to the reversal phase. In the P reversal, the colour which had been rewarded during the acquisition phase now ceased to be rewarded and a newly introduced colour became the rewarded stimulus. In the LNR condition, the formerly unrewarded colour was rewarded in the reversal phase while a newly introduced colour became the unrewarded stimulus.



**Figure 3.1** Illustration of the perseverance (P) and learned non-reward (LNR) reversal designs. In both the acquisition and reversal phases, a subject must learn to choose the rewarded (+) colour stimulus: in the reversal phase of the P condition, the previously rewarded colour is unrewarded while in the reversal phase of the LNR condition, the previously unrewarded colour (-) is rewarded. Each reversal incorporates a newly introduced colour (grey). The colours used for this illustration were actually used for some subjects, but other colour combinations were also used to ensure that the outcome is not confounded with any single colour combination (see Appendix 5).

One half of the birds were tested in the P condition first, while the other half received the LNR condition first. The colour stimuli used in the two conditions differed. Table A5 (Appendix 5) gives an overview of the counterbalanced use of colour stimuli in both phases of each of the two learning conditions.

To assess learning success for each subject in the LNR and P reversal conditions, the number of trials to reach success criterion and the total number of errors in both acquisition and reversal phases were measured. Eight woodpecker finches and 8 small tree finches were tested in the P and LNR reversal conditions.

**Test apparatus** The apparatus was a two-choice setup. It consisted of two white plastic boxes (3 x 2 x 2.3cm each), which were affixed 10 cm apart from each other on a wooden board (20 x 20cm) and separated by a clear Perspex divider (29.5 x 21cm). Each box was covered with a coloured foam lid which had to be removed to obtain a food reward that was hidden in one of the two boxes.

**Training** Before testing, all birds were trained to remove the lids and obtain rewards from the boxes. In the training procedure, subjects were presented with a single white box (with the same dimensions as the boxes used in the actual experiment), which was affixed to a small wooden block and covered with a piece of white cardboard. They were trained to remove the lid from the box by a shaping procedure and were deemed to have learned this reliably once they had retrieved the food reward from the box in 6 consecutive trials within two minutes.

**Testing procedure** The bird was given up to 5 minutes to remove one of the lids and obtain the reward from the baited apparatus. If the bird removed one of the lids, the apparatus was taken from the aviary and re-baited if necessary. Rewarded sides were pseudo-randomized and counterbalanced right and left, but a reward was never presented on the same side more than three times in a row (exception: side bias correction procedure, see below). Birds were tested in sessions of 20 trials. However, if a bird was close to attaining the learning criterion (see below) at the end of a session and only one correct trial away from completing a testing phase, it was given one additional trial. The subjects received two sessions per day and a maximum of 140 trials total in each phase of each learning condition.

**Learning Criterion** A bird met the learning criterion, when it chose the rewarded stimulus at least 15 times within two consecutive blocks of 10 trials. More specifically, in two blocks of 10 trials it had to make either 7 correct responses in a row in one block and in the other block 8 or more, or, alternatively, it had to make 10 correct responses in a row.

**Re-habituation** When a bird did not open either of the boxes within 5 minutes, it was given a re-habituation trial in which the lids were removed from the boxes and both boxes contained a food reward. If the bird fed from the boxes within 5 minutes, the previous trial was repeated and the testing session was resumed. If not, testing was ended for that session. Furthermore, a bird never received more than 2 re-habituation trials per session: if it did not

approach the apparatus within 5 minutes for a third time, the session was also terminated.

**Side bias correction** We determined that a subject had developed a side bias when it chose the same side of the apparatus for 6 trials in a row. In this case, rewards were only placed on the non-preferred side in the following trials, until the bird chose the non-preferred side once. After this, the normal schedule was resumed.

### *Reactions to novelty*

We used two standard experimental designs to assess the two components of reaction to novelty namely “latency to approach a novel object” for neophilia (e.g. Raach and Leisler 1989; Verbeek et al. 1994) and “latency to feed near novel objects” for neophobia (Greenberg 1984). As an additional measure for neophobia we used “latency to feed from a novel apparatus”. Testing started between 11-72 days after release into the aviaries and the length of this period did not differ between species (small tree finches: median = 17.5 days to testing, range = 12-53 days; woodpecker finches: median = 38 days, range = 11-72 days; Mann-Whitney U-test:  $N_{sf} = 14, N_{wp} = 10, U = 43.0, p = 0.122$ )<sup>1</sup>.

**Neophobia (feeding near novel objects)** To assess neophobia, a novel object was placed in the home aviary directly next to the familiar feeding dish (containing the normal food) on the experiment table and the latency to start feeding was recorded. All feeding latencies were measured during the morning feeding routine. At that time, birds had been food-deprived overnight (at least 12 hours) and presumably had a similar hunger level. Thus, a high motivation to feed should at this time have outweighed most exploratory tendencies and thus have only been opposed by neophobia. Therefore, feeding latencies near the novel objects should reflect relative neophobia levels.

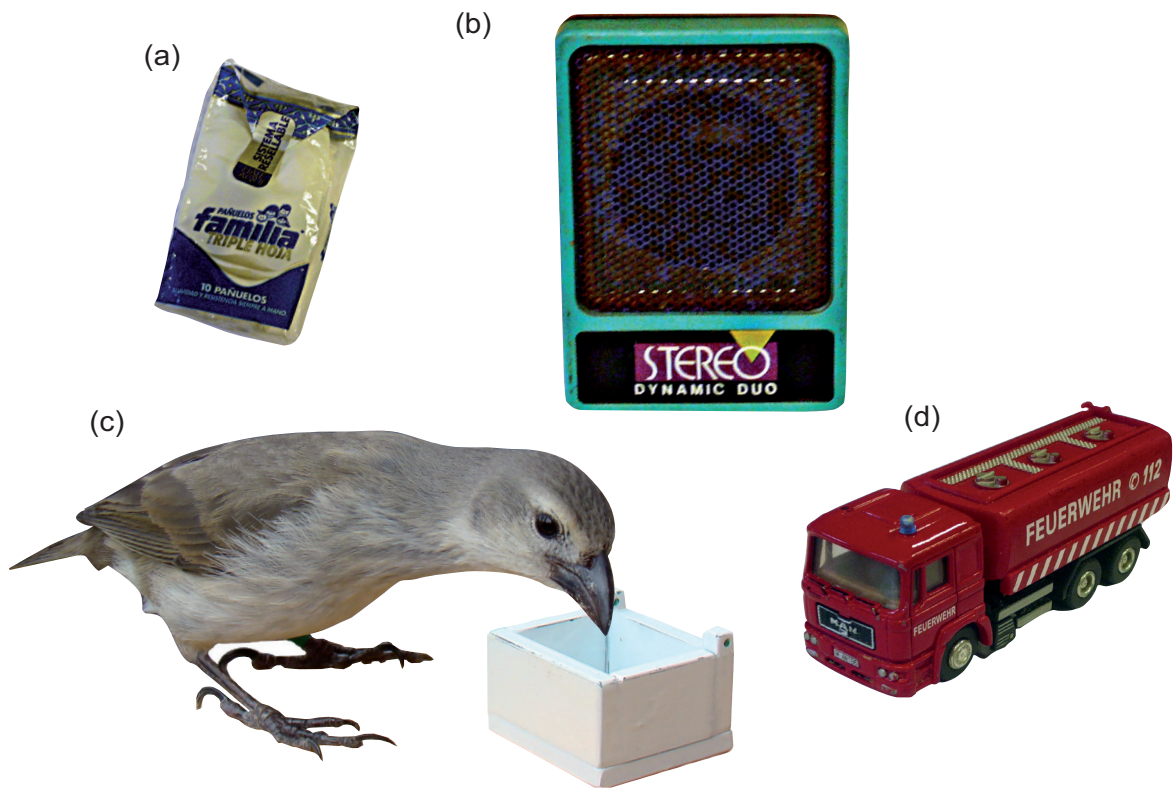
Subjects were tested once with each of two novel objects. Birds were first tested with the smaller, less colourful novel object which was a blue and white tissue package (1.5 x 6.5 x 2.5cm, Figure 3.2a). One to five days later, the birds were tested with a green, purple and black loudspeaker (7 x 7.5 x 10cm, Figure 3.2b).

Control feeding latencies of all birds in undisturbed conditions were determined by measuring the latency to feed from the familiar feeding dish on the experiment table when first given food in the morning. To find out which of the two novel objects evoked fearful responses in each species, feeding latencies in the control situation were compared to those of the novel object experiments.

For the species comparison we subtracted the control feeding latency from each of the latencies to feed near the novel objects. As only the loudspeaker elicited fearful reactions in both species we were only able to use this experimental condition to detect a species dif-

---

<sup>1</sup> For Mann-Whitney U-tests, sample sizes of the comparison groups are given with a subscript denoting species group (sf=small tree finches, wf=woodpecker finches).



**Figure 3.2** Objects used in measuring novelty reactions. A (a) tissue package, (b) loudspeaker, and (c) novel apparatus from operant task were used in neophobia tasks and a (d) toy car was used to test neophilia. A woodpecker finch is pictured in order to give an approximation of the size of the objects compared with the birds.

ference. Ten woodpecker finches were tested with both novel objects while 15 small tree finches were tested with the tissue package and 16 with the loudspeaker.

**Neophobia (feeding from a novel apparatus)** Since woodpecker finches did not show differences in their reaction to novelty in the tissue experiment, we included measurements taken from the first training session of an operant task (Chapter 1) as an additional measure of neophobia (Figure 3.2c). Birds were deprived 2 hours prior to their first training session. The session began with presentation of a food reward in a novel apparatus. The apparatus was the white plastic box that was later used in an operant task (see below). The box was baited with a food reward and placed on the experiment table with the lid open for up to 25 minutes. Latencies to feed from the box were measured. If a subject did not feed from the novel apparatus in 25 minutes, it was given a ceiling value of 1801 seconds. Only 4 of the small tree finches fed from the box within 25 minutes, so latencies to feed from the box could not be compared between species. Instead, we compared the numbers of individuals that fed from the box within 25 minutes between species. Ten woodpecker finches and 8 small tree finches participated in this test.

**Neophilia** In this experiment we measured latency to approach and touch a novel object. The novel object was a red toy car (11 x 3 x 4.5cm), which was placed in the middle of the experiment table for up to 30 minutes (Figure 3.2d). In this test, subjects were not food-deprived before or during testing, so neophilia and not hunger was assumed to be the driving motivation of any exploratory activity. Latencies to hop on the perch above the experiment table, to hop onto the table itself and to touch the car were measured. The experiment was ended when a bird touched the car or when it exceeded the maximum session length of 30 minutes. Each bird received one session. Ten woodpecker finches and 16 small tree finches participated in this experiment. Only 28.6% of the woodpecker finches and 25% of the small tree finches touched the novel object. To have a suitable measure that comprises as many individuals as possible, only the first step of approach towards the novel object which allowed closer visual inspection of the novel object requiring an approach at eye-level (the latency to hop onto the perch), was analyzed. Within the duration of the experiment time, 8 out of 10 woodpecker finches and 13 out of 16 small tree finches approached the toy car. All subjects that did not come to the perch or the table were assigned a ceiling value of 1801 seconds.

## Data Analysis

### *Reversal learning performance*

The analysis of the LNR and P reversal data was conducted with R (R development core team 2010, version 2.12.0).

**Between-species comparison** To analyze species differences in the learning experiments, we ran two-way within-subjects ANOVAs using the “aov” function of the “stats package. We chose two response variables that reflected learning performance: “number of trials to success” and “proportional errors”, which was the proportion of errors to the number of trials needed to meet the success criterion in each learning phase. A separate model was run for each condition (LNR and P), and also for each response variable reflecting learning. Each model consisted of the response variable and two categorical explanatory variables: “phase” a factor with two levels (acquisition and reversal phase) and “species” (woodpecker finches and small tree finches). In all models, an error term in which phase was nested within subject was specified. The models consisted of the main effects of phase and species as well as the second order interaction between them. We report the results of the main effects only when there was not a significant interaction between the two explanatory variables. An interaction suggested that there was a difference in the reversal performance between species that was dependent on the acquisition performance while a main effect of phase indicated that overall performance in the two phases differed significantly. A main effect of species indicated that there was a significant difference in overall performance depending on the level of species.

**Within-species comparison** We also wanted to know whether one of the experiments was more difficult than the other for each species. To investigate this, we again used the “aov” function of the “stats” package to compare performance between the two reversal learning conditions (LNR and P) within species. The same response variables were used (“trials to success” and “proportional errors”) but this time, each species was analyzed separately. The explanatory variables were “phase” and “condition”, a factor with two levels: LNR and P. The error term consisted of phase nested within condition, which was in turn nested within subject.

Models were constructed with the main effects “phase” and “condition” and the second order interaction between them. An interaction would have indicated that the difficulty of the reversal phase with respect to the acquisition phase was different in the two experiments for the species being analyzed. A significant main effect of phase indicated that overall, performance differed significantly between phases while a significant main effect of experiment indicated that the given species performed overall better in one of the experiments than in the other (but not necessarily only in the reversal phase).

**Assessing the effect of experience on simple discrimination learning** The acquisition phase of each of the two conditions (LNR and P) presented exactly the same problem, namely a simple colour discrimination task. To see if birds improved simple discrimination learning with increasing experience, we also compared performance only of the acquisition phases of the LNR and P conditions according to the levels of species. To this end, we constructed a model separately with proportional errors and trials to success. The model included the main effects of species and order as well as the interaction between them. The error term consisted of order nested within subject. We were interested in a main effect of order which would have suggested a significant difference in overall performance between the first and second acquisition phases. Furthermore, an interaction between order and species would have indicated that there was a difference in performance in the first and second acquisitions between species.

**Assessing the effect of novelty reactions on learning performance** Because reaction to novelty could play a role in solving the reversal tasks in which new colours appear alongside familiar ones, the trial number at which each subject chose the novel colour for the first time in each reversal regime was compared between species and within species between reversal conditions using the Mann-Whitney U-test (two-tailed). This test and all other statistical analyses described in the following were conducted with SPSS 15.0.

### *Novelty reactions*

**Neophobia** To assess which of the novel objects incited a strong neophobic reaction, we compared feeding latencies in the presence of each of the novel objects with baseline feeding latencies separately for each species using Wilcoxon signed ranks tests (two-tailed). To

compare neophobia between species, the values attained by subtracting the control feeding latency from the latency to approach the loudspeaker were compared using the Mann-Whitney U-test (two-tailed). It was not possible to compare feeding latencies from the novel apparatus between species since so few small tree finches actually fed from the apparatus. Therefore, the Fisher's exact test (two-tailed), a contingency test that is commonly used when dealing with small sample sizes, was used to test for a significant difference in the proportion of individuals that solved this task (fed from the novel apparatus) between species.

**Neophilia** The Mann-Whitney U-test (two-tailed) was used to compare the latencies to approach the toy car between species.

**Consistency of neophobic responses** To test whether the neophobic reaction of individuals was consistent, we used the Spearman's rank correlation test (two-tailed) and tested the relationship between repeated measures of neophobia for each species. For small tree finches, the measures "latency to feed near the tissue package" and "latency to feed near the loudspeaker" were used for this correlation. However, since the tissue package did not evoke a neophobic reaction in woodpecker finches, the "latency to feed near the loudspeaker" and "latency to feed from the novel box" were used to test the consistency of neophobic reaction in this species.

### *Investigating relationships between measured behaviour*

**Neophobia and neophilia** Two-tailed Spearman's rank correlation tests were used to investigate the relationship between the latency to feed near the loudspeaker and to approach the toy car separately for the two species.

**Novelty reactions and reversal learning** To assess the relationship between reversal learning and novelty reactions, we conducted two-tailed Spearman's rank correlation tests with data reflecting reversal learning performance (reflected by proportional errors and trials to success) and measures reflecting neophobia and neophilia separately for each species and also for the LNR and P reversal conditions. We also correlated proportional errors and trials to success in the reversal phase of the classical reversal task of the previous study (Tebich et al. 2010) with measures of novelty reactions. In these correlations, latency to approach the loudspeaker was used as the measure for neophobia since this was the only neophobia measure for which we had a comparable measure for both species in this experiment.

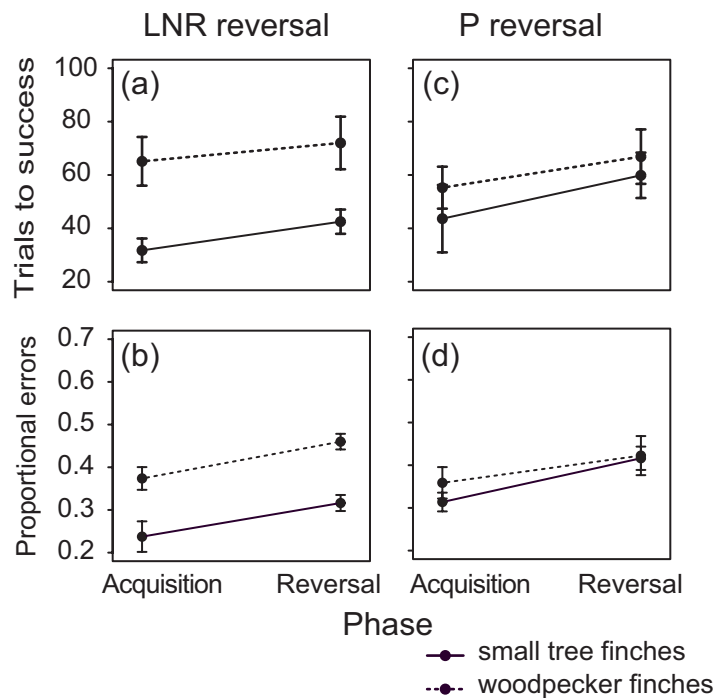
It should be noted that neophobia (as measured by the loudspeaker) and neophilia (measured with the toy car) was also measured for 8 additional woodpecker finches from the Arid zone for another study. Because animals in these two zones experience substantially different seasonal and annual fluctuation in resources that could influence novelty reactions and learning differences, only data for woodpecker finches from the Scalesia zone is reported in the direct species comparisons of this study. However, since the classical reversal learning

and novelty reaction correlations were not conducted as a direct species comparison, rather their purpose was to test the general relationship between learning performance and reaction to novelty, we used all the available data for woodpecker finches from both zones.

## RESULTS

### Reversal learning performance

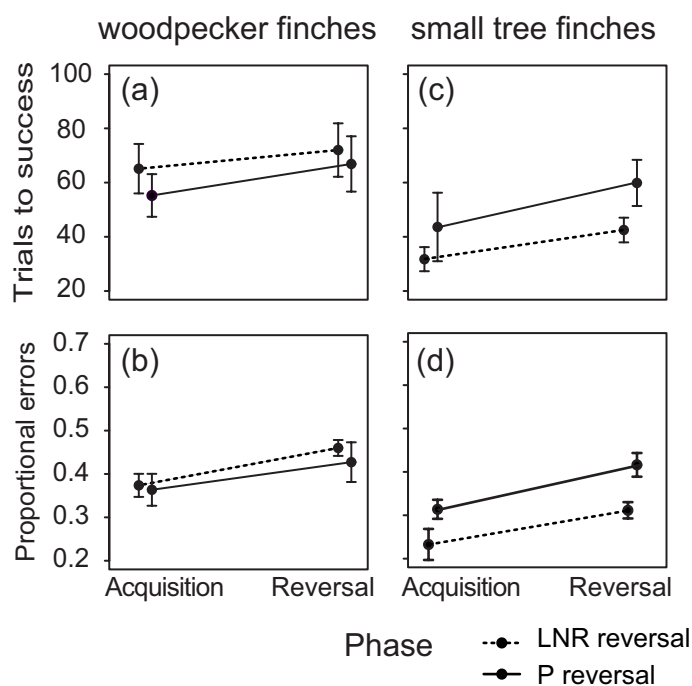
**Between-species comparison** In the LNR reversal condition, performance in the reversal phase compared with the performance in the acquisition phase did not differ between species (species\*phase for trials to success:  $F_{1,14} = 0.07, p = 0.796$ , Figure 3.3a; proportional errors:  $F_{1,14} = 0.03, p = 0.876$ , Figure 3.3b). However, small tree finches required less trials to meet the criterion in both phases (main effect of species:  $F_{1,14} = 17.60, p < 0.001$ , figure 3a) and made less proportional errors overall in doing so in both phases than woodpecker finches (main effect of species:  $F_{1,14} = 25.00, p < 0.001$ , Figure 3.3b). Furthermore, neither woodpecker finches nor small tree finches needed more trials to success in the reversal phase than in the acquisition phase (main effect of phase:  $F_{1,15} = 1.52, p = 0.236$ , Figure 3.3a) but subjects of both species made more proportional errors in the reversal phase than in the acquisition phase (main effect of phase:  $F_{1,15} = 13.14, p < 0.01$ , Figure 3.3b).



**Figure 3.3** Between-species comparison of reversal learning performance (mean  $\pm$  S.E.M.) in terms of trials to success (a,c) and proportional errors (b,d) in the acquisition and reversal phases of the LNR (a,b) and P (c,d) reversal conditions.

In the P condition, there was no significant difference between species in reversal phase performance compared with acquisition performance either in terms of the trials to success (species\*phase:  $F_{1,14} = 0.08$ ,  $p = 0.781$ , Figure 3.3c) or proportional errors ( $F_{1,14} = 0.55$ ,  $p = 0.470$ , Figure 3.3d). We also found no indication for an overall species difference in learning performance (main effect of species for trials to success:  $F_{1,14} = 0.65$ ,  $p = 0.432$ , Figure 3.3c; for proportional errors:  $F_{1,14} = 0.40$ ,  $p = 0.540$ , Figure 3.3d). Finally, there was no significant difference in performance between phases for either species in terms of trials to success ( $F_{1,15} = 3.11$ ,  $p = 0.098$ , Figure 3.3c), but highly significantly more proportional errors were made in the acquisition phase than in the reversal phase ( $F_{1,14} = 10.49$ ,  $p = 0.006$ , Figure 3.3d).

**Within-species comparison** Compared to the respective acquisition tasks, woodpecker finches did not differ significantly in their learning performance in the P and LNR reversal conditions (condition\*phase for trials to success  $F_{1,14} = 0.06$ ,  $p = 0.803$ , Figure 3.4a; proportional errors:  $F_{1,14} = 0.19$ ,  $p = 0.673$ , Figure 3.4b). Furthermore, there was no significant overall difference in performance between the LNR and P conditions (acquisition and reversal phase combined) for woodpecker finches (main effect of condition for trials to success:  $F_{1,7} = 0.50$ ,  $p = 0.504$ , Figure 3.4a; and proportional errors:  $F_{1,7} = 0.46$ ,  $p = 0.520$ , Figure 3.4b). However, woodpecker finches made more proportional errors in the reversal phases than in the acquisition phases in both conditions (main effect of phase:  $F_{1,15} = 8.72$ ,  $p = 0.010$ , Figure

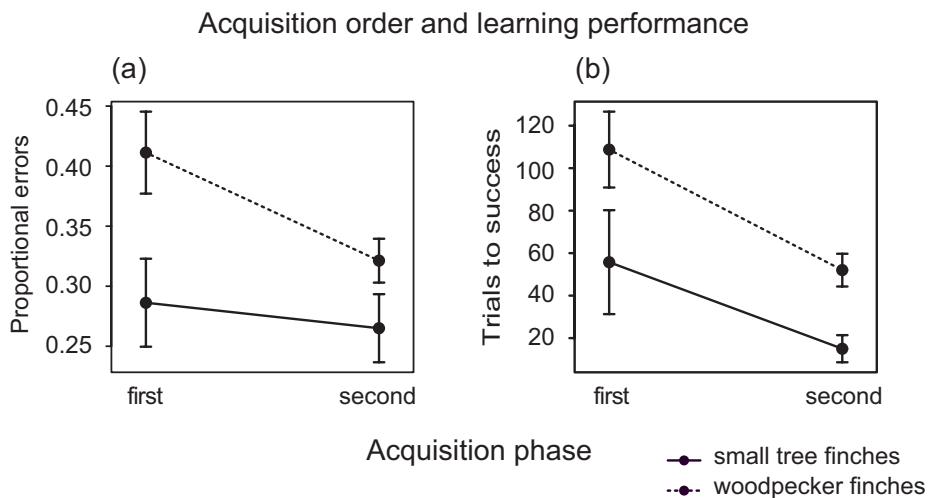


**Figure 3.4** Within-species comparison of reversal learning performance (mean  $\pm$  S.E.M.) for woodpecker finches (a,b) and small tree finches (c,d) in terms of trials to success (a,c) and proportional errors (b,d) for both phases of the LNR and P reversal conditions.

3.4b) though they did not need more trials to reach the success criterion ( $F_{1,15} = 1.05$ ,  $p = 0.323$ , Figure 3.4a).

Small tree finches, also did not find one of the reversal conditions more difficult to learn than the other compared to the acquisition task (condition\*phase for trials to success  $F_{1,14} = 0.23$ ,  $p = 0.642$ , Figure 3.4c; proportional errors  $F_{1,14} = 0.26$ ,  $p = 0.621$ , Figure 3.4d). Overall, the number of trials they needed to meet criterion did not differ between phases according to condition (main effect of condition:  $F_{1,7} = 2.13$ ,  $p = 0.187$ , Figure 3.4c), though they made significantly less proportional errors overall in the LNR than in the P condition (main effect of condition:  $F_{1,7} = 6.85$ ,  $p = 0.035$ , Figure 3.4d). According to both measures of learning, small tree finches always found the acquisition phase easier to learn than the reversal phase (main effect of phase for trials to success:  $F_{1,15} = 5.72$ ,  $p = 0.030$ , Figure 3.4c; proportional errors:  $F_{1,15} = 15.68$ ,  $p = 0.001$ , Figure 3.4d).

**Assessing the effect of experience on simple discrimination learning** The investigation of the effect of experience on learning in the acquisition phase revealed that overall, birds were significantly faster (main effect of order:  $F_{1,15} = 10.47$ ,  $p = 0.006$ , Figure 3.5b) and there was a tendency to make less proportional errors ( $F_{1,15} = 3.52$ ,  $p = 0.080$ , Figure 3.5a) in the second acquisition compared to the first. There was a species difference in overall performance in the two acquisitions (main effect of species for trials to success:  $F_{1,14} = 7.49$ ,  $p = 0.016$ ; proportional errors:  $F_{1,14} = 8.51$ ,  $p = 0.011$ ) with small tree finches outperforming woodpecker finches in both measures of learning (Figure 3.5a,b). However there was no species difference in the amount of improvement in the second acquisition phase with respect to the first (species\*order for trials to success:  $F_{1,14} = 0.27$ ,  $p = 0.613$ ; proportional errors:  $F_{1,14} = 1.38$ ,  $p = 0.260$ , Figure 3.5b,a).



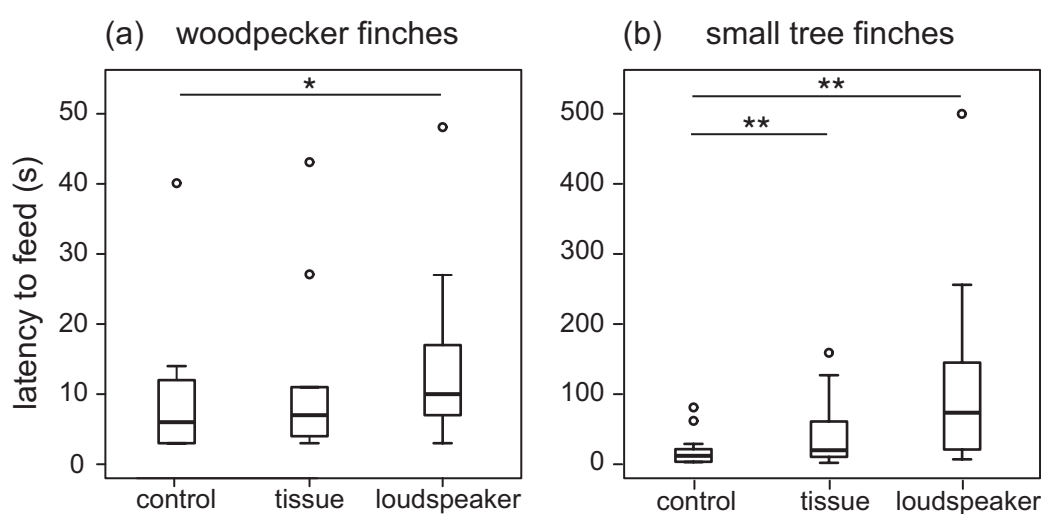
**Figure 3.5** Comparison of learning performance in terms of (a) proportional errors and (b) trials to success (mean  $\pm$  S.E.M.) in the first and second acquisition phase experienced between species.

**Assessing the effect of novelty reactions on learning performance** Both woodpecker finches and small tree finches picked the new colour very early in each reversal learning block: 78.1% of the individuals chose it for the first time within the first 3 trials. There was no significant difference between species in the trial number at which they picked the new colour for the first time in either the LNR (small tree finches: median = 1.5, range = 1-5; woodpecker finches: median = 1, range = 1-2; Mann-Whitney U-test:  $U = 19.0$ ,  $N_{sf} = 8$ ,  $N_{wf} = 8$ ,  $p = 0.195$ ) or the P condition (small tree finches: median = 1.5, range = 1-12; woodpecker finches: median = 3, range = 1-7; Mann-Whitney U-test:  $U = 26.0$ ,  $N_{sf} = 8$ ,  $N_{wf} = 8$ ,  $p = 0.574$ ).

## Novelty reactions

**Neophobia (feeding near novel objects)** Woodpecker finches did not significantly increase their feeding latencies in the presence of the tissue package (Wilcoxon test:  $z = -1.05$ ,  $N = 10$ ,  $p = 0.292$ ) but reacted with a significant increase in feeding latencies near the loudspeaker compared to their control feeding latencies (Wilcoxon test:  $z = -2.55$ ,  $N = 10$ ,  $p = 0.011$ , Figure 3.6a). Small tree finches fed significantly later in the presence of both the tissue package (Wilcoxon test:  $z = -2.91$ ,  $N = 16$ ,  $p = 0.004$ ) and the loudspeaker (Wilcoxon test:  $z = -3.39$ ,  $N = 16$ ,  $p = 0.001$ ) than in the control condition (Figure 3.6b).

In the interspecific comparison of the difference between responses to the loudspeaker and control condition, small tree finches exhibited a highly significantly stronger reaction towards this novel object than woodpecker finches (Mann-Whitney U-test:  $U = 21.0$ ,  $N_{sf} = 16$ ,  $N_{wf} = 10$ ,  $p = 0.001$ ).



**Figure 3.6** Comparison of neophobia to a control feeding latency. Feeding latencies reflecting neophobia were measured when subjects fed in the presence of an unfamiliar tissue package or loudspeaker to baseline (control) feeding latencies in seconds for (a) woodpecker finches and (b) small tree finches.

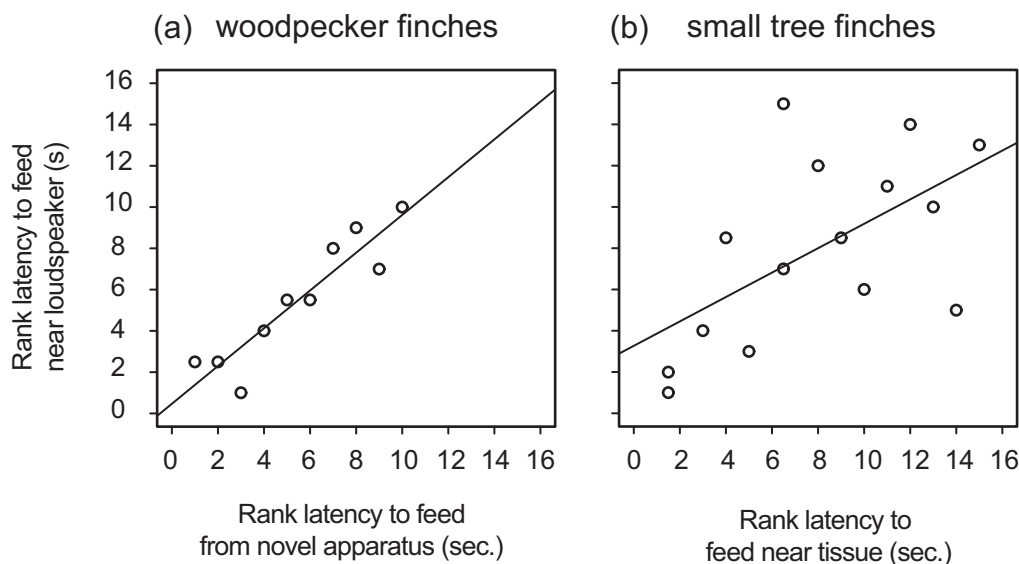
**Neophobia (feeding from novel apparatus)** Only 4 out of 8 tested small tree finches, but 9 out of 10 woodpecker finches fed from the novel apparatus within 25 minutes. Nevertheless, this difference between species was not significant (Fisher's exact test:  $p = 0.484$ ).

**Neophilia** Small tree finches (median = 371 seconds, range = 0-1801) and woodpecker finches (median = 329 seconds, range = 1-1801) did not differ significantly in their latencies to approach a novel object (toy car) in their home aviary (Mann-Whitney U-test:  $U = 74.5$ ,  $N_{sf} = 16$ ,  $N_{wf} = 10$ ,  $p = 0.776$ ).

**Consistency of neophobic responses** Individuals of both species showed consistent neophobic behaviour in the different neophobia tasks they were tested in. For woodpecker finches, latencies to feed near the loudspeaker and to feed from the novel apparatus task correlated positively (Spearman's correlation:  $\rho = 0.92$ ,  $N = 10$ ,  $p < 0.0001$ , Figure 3.7a), whereas for small tree finches there was a positive correlation between feeding near the tissue package and feeding near the loudspeaker (Spearman's correlation:  $\rho = 0.59$ ,  $N = 15$ ,  $p = 0.020$ , Figure 3.7b).

## Investigating relationships between behavioural measures

**Neophobia and neophilia** Latency to feed near the loudspeaker and latency to approach the toy car were not correlated significantly either in the woodpecker finches (Spearman's correlation:  $\rho = -0.08$ ,  $N = 10$ ,  $p = 0.828$ ) or the small tree finches tested (Spearman's correlation:  $\rho = 0.37$ ,  $N = 16$ ,  $p = 0.157$ ).



**Figure 3.7** Consistency of neophobic responses. For (a) woodpecker finches, consistency was measured between latency to feed from the novel apparatus and near the loudspeaker whereas for small tree finches (b), consistency was measured between latency to feed near the loudspeaker and near the tissue package.

**Table 3.1** (a) Spearman's correlations between neophobia (measured as latency to feed near an unfamiliar loudspeaker in seconds) and reversal learning, as measured by trials to success needed and proportional errors made in meeting criterion. Correlations were conducted separately for the classical, P and LNR reversal conditions. (b) Correlations between neophilia (latency to approach toy car in seconds) and reversal learning in the three reversal conditions.

Species <sup>1</sup>	Learning condition and phase <sup>2</sup>	Measure of learning	N	Spearman's Rho	p
<i>(a) Relationship between reversal phase performance and neophobia</i>					
WPF	Classical reversal	proportional errors	16	-0.603	<b>0.013</b>
WPF	Classical reversal	number of trials	16	-0.474	0.064
STF	Classical reversal	proportional errors	8	-0.024	0.955
STF	Classical reversal	number of trials	8	-0.679	0.064
WPF	LNR reversal	proportional errors	8	-0.359	0.382
WPF	LNR reversal	number of trials	8	-0.755	<b>0.031</b>
STF	LNR reversal	proportional errors	8	0.048	0.910
STF	LNR reversal	number of trials	8	0.139	0.744
WPF	P reversal	proportional errors	8	-0.036	0.933
WPF	P reversal	number of trials	8	-0.777	<b>0.023</b>
STF	P reversal	proportional errors	8	-0.132	0.756
STF	P reversal	number of trials	8	0.464	0.247
<i>(b) Relationship of reversal phase performance and neophilia</i>					
WPF	Classical Reversal	proportional errors	16	-0.180	0.505
WPF	Classical Reversal	number of trials	16	0.088	0.747
STF	Classical Reversal	proportional errors	8	-0.671	0.069
STF	Classical Reversal	number of trials	8	-0.451	0.262
WPF	LNR Reversal	proportional errors	8	0.381	0.352
WPF	LNR Reversal	number of trials	8	-0.048	0.911
STF	LNR Reversal	proportional errors	8	-0.405	0.320
STF	LNR Reversal	number of trials	8	-0.467	0.243
WPF	P Reversal	proportional errors	8	1.000	1.000
WPF	P Reversal	number of trials	8	0.156	0.713
STF	P Reversal	proportional errors	8	0.619	0.102
STF	P Reversal	number of trials	8	-0.323	0.435

<sup>1</sup> STF = small tree finches, WPF = woodpecker finches

<sup>2</sup> reversal = reversal phase

**Table 3.2** Relationship between the number of positive reinforcements in the acquisition phase of each of the three reversal conditions and neophobia (latency to feed near an unfamiliar loudspeaker in seconds).

Species <sup>1</sup>	Task and phase <sup>2</sup>	Measure of positive reinforcement	N	Spearman's Rho	p
WPF	Classical acquis.	# successful choices	16	-0.074	0.785
STF	Classical acquis.	# successful choices	8	-0.515	0.192
WPF	P acquis.	# successful choices	8	-0,025	0.949
STF	P acquis.	# successful choices	8	0.193	0.647
WPF	L acquis.	# successful choices	8	0.455	0.257
STF	L acquis.	# successful choices	8	-0.618	0.102

<sup>1</sup>STF = small tree finches, WPF = woodpecker finches

<sup>2</sup>acquis. = acquisition phase

**Novelty reactions and reversal learning** For the classical reversal task we found a significant negative correlation between neophobia (latency to feed near the loudspeaker) and proportional errors but not for number of trial to success in woodpecker finches (Table 3.1a). However, in small tree finches we did not find a significant correlation for either measure of reversal learning from the classical reversal learning task and neophobia (Table 3.1a).

For woodpecker finches, we found negative correlations between neophobia and the LNR reversal learning speed (Spearman's correlation:  $\rho = -0.755$ ,  $N = 8$ ,  $p = 0.031$ , Table 3.1a), as well as between neophobia and learning speed in the P reversal (Spearman's correlation:  $\rho = -0.777$ ,  $N = 8$ ,  $p = 0.023$ , Table 3.1a), meaning that in both conditions more neophobic individuals learn more quickly. However, the correlations between neophobia and proportional errors in the LNR and P reversal were non-significant for woodpecker finches. In the case of small tree finches, neophobia did not correlate with either of the two measures for reversal learning in the LNR or the P reversal. Neophilia did not correlate with reversal learning in any of the three reversal learning experiments (Table 3.1b).

It is possible that neophobic birds received less reinforcement in the acquisition phase and therefore show faster extinction of the learned association in the reversal phase. However, we did not find a correlation between latency to feed near the loudspeaker and number of positive reinforcements in the acquisition phase (Table 3.2).

## DISCUSSION

Contrary to the predictions, woodpecker finches were not slower at learning the P reversal than the LNR reversal when compared with the respective acquisition phases. Indeed, there

were no significant differences in woodpecker finch performance for either phase of the LNR or P conditions. The comparison of woodpecker finches and small tree finches also did not yield the expected outcome: woodpecker finches were not outperformed by small tree finches in the P reversal phase compared with their performance in the acquisition phase. Though small tree finches clearly outperformed woodpecker finches in the LNR reversal phase, a difference in performance was already observable in the acquisition phase, thus the disparity in performance cannot be attributed to a species-difference in the difficulty of the reversal problem. Small tree finches also performed better overall in the LNR condition than the P condition (though the difference was only significant for proportional errors) but again since the difference was observed in both phases, it cannot be inferred that one type of reversal was easier than the other.

Overall, small tree finches were better in both acquisition phases of this study than woodpecker finches. A between-species difference in the acquisition phase is puzzling because it indicates a difference in simple colour discrimination learning that we did not find in the classical reversal experiment which had been conducted in the previous study (Chapter 1, Experiment 1).

The disparity in performance that we find in the current study could be due to different holding conditions of the two species: the woodpecker finches already had spent a year in captivity before being tested in the new reversal conditions while the small tree finches were only caught and placed into captivity a few weeks prior to testing. The stable food situation in captivity might have influenced the speed of learning via motivation. However, since different holding conditions would very likely affect both the acquisition and reversal phases, results based on the difference between these phases should not be affected. In sum, our data did not support the hypothesis that differences in reversal learning between woodpecker finches and small tree finches were due to a more persistent choice of the previously rewarded stimulus by woodpecker finches.

Reaction to novelty can also affect learning in various ways. In particular, it is conceivable that the introduction of a new colour stimulus in the reversal phases in the LNR and P conditions might have strongly impacted the outcome of the experiment. Avoidance or affinity towards the novel colour in each reversal phase could have had opposing effects on learning performance in the LNR and P reversal; a highly neophilic reaction towards the novel colour would enhance learning in the P reversal, because here the novel colour was rewarded. On the other hand, performance in the LNR reversal could have been depressed because in this condition the novel colour was the unrewarded stimulus. Conversely, species that showed higher neophobia when confronted with the novel stimulus would have been expected to have delayed choosing this stimulus compared to individuals of the less neophobic species. We found no species difference in neophilia but in our neophobia experiments, woodpecker finches were less neophobic than small tree finches. This is in line with findings from studies on primates (Day et al. 2003; Vitale et al. 1991), in which species relying on extractive or manipulative foraging were less neophobic than closely related non-extractive

foragers. Thus, attraction towards the novel stimulus could have improved the performance of woodpecker finches in the P condition and thus have masked opposing effects of perseverance. However, since there was no significant between-species difference in the trial numbers at which they chose the novel colours for the first time, reaction to novelty is not likely to play a role in this context.

Differences in the neophobic reaction are nevertheless interesting in their own right. Neophobia is thought to be driven by the costs of exploration, such as predation (Greenberg and Mettke-Hofmann 2001). Thus, a higher predation pressure on small tree finches compared to woodpecker finches could be an explanation for their increased neophobia. Interestingly, some findings indicate that small tree finches actually suffer from predation by Short-eared Owls (*Asio flammeus galapagoensis*) while woodpecker finches do not (De Groot 1982) though Abs et al. (1965) listed woodpecker finches, as well as most other species of Darwin's Finches, as prey of the Short-eared Owl. Grant (1986) noted that owls generally prefer smaller birds, which makes small tree finches more vulnerable to predation than woodpecker finches due to their smaller body size.

Despite species differences in neophobia, the relative levels of individual neophobia were consistent within individuals across different neophobia experiments which indicates that in these two Darwin's finch species, reaction to novelty can be seen as part of an individual's general coping style (Dingemanse et al. 2002; Drent and Marchetti 1999; Verbeek et al. 1994). This is relevant for this study on reversal learning since previous work on great tits revealed a link between reaction to novelty and reversal learning (Marchetti and Drent 2000; Verbeek et al. 1994). In both studies, individuals that were slower in exploring novel objects or novel environments were faster at changing non-productive feeding locations than their less neophobic conspecifics.

Using the data from our classical reversal experiment, we also found a negative correlation between proportional errors in the reversal phase and neophobia in woodpecker finches but not in small tree finches. We found no significant correlation between any of the reversal tests and the latency to approach the object in the neophilia test.

Learning performance in the new reversal conditions (LNR and P) correlated negatively with neophobia but only for woodpecker finches and only for number of trials to success. No significant correlations were found for small tree finches. This could be due to the low sample sizes and a low variance in small tree finches regarding the number of trials and errors to success. The finding of a significant correlation between learning speed and neophobia in *both* reversal conditions, suggests that neither persistency nor difficulties in responding to a formerly unrewarded stimulus alone are likely to account for the relationship with neophobia. Instead, at least in woodpecker finches, slow explorers seem to be faster at unlearning both components of the reversal learning problem and the relationship does not seem to be driven directly by reaction to novelty but by other components of the coping style.

On the interspecific level, we found the same negative relationship between neophobia and reversal learning: small tree finches were faster in acquisition and reversal learning

and were significantly more neophobic than woodpecker finches. This suggests a common mechanism accounting for differences both within and between species. For instance, faster extinction of learned associations in neophobic birds (on the individual as well as the species level) could favour a higher speed of reversal learning. Drent and Marchetti (1999) suggested that less neophobic birds visit a reinforced stimulus more often and therefore the learned association extinguishes slower. However we did not find a correlation between latency to feed near a novel object and number of positive reinforcements in the acquisition phase either in the current study or the classical reversal experiment.

To summarize, our study could not confirm that woodpecker finches show more perseverance in choosing a previously rewarded stimulus. Therefore, we cannot invoke this as an explanation for the depressed performance of woodpecker finches compared to small tree finches in the classical reversal learning task (Chapter 1, Experiment 1). An alternative explanation is that the performance of woodpecker finches is not depressed, rather small tree finches might be particularly proficient reversal learners for unknown reasons. More detailed experiments are needed to explain why small tree finches are better at reversal learning and also why in several species slow explorers are better at unlearning previously learned rules.

## **ACKNOWLEDGEMENTS**

IT was supported by the German research foundation (DFG, Project Nr. TE628/1-1) and ST by the Austrian Science Fund (FWF, Project Nr. V95-B17). The experiments comply with the current laws of the country in which they were performed. We are thankful to the Charles Darwin Research Station for support and TAME for reduced ticket fares. We are also grateful to Dr. Birgit Fessl for support in all facets of this study. Tania Quisingo Chiza, Paola Buitron Lopez, and Eduardo Sandoval provided valuable field assistance and help with experiments. Patrick Meidl provided vital support in organizing vast amounts of data.



## CHAPTER 4



# THE TALE OF THE FINCH: ADAPTIVE RADIATION AND BEHAVIOURAL FLEXIBILITY

Tebbich, S., Sterelny, K. and Teschke, I.  
(2010) *Phil. Trans. R. Soc. Lond. B.* 365: 1099–1109.

### Abstract

*Darwin's finches are a classic example of adaptive radiation. The ecological diversity of the Galápagos in part explains that radiation, but the fact that other founder species did not radiate suggests that other factors are also important. One hypothesis attempting to identify the extra factor is the flexible stem hypothesis, connecting individual adaptability to species richness. According to this hypothesis, the ancestral finches were flexible and therefore able to adapt to the new and harsh environment they encountered by exploiting new food types and developing new foraging techniques. Phenotypic variation was initially mediated by learning, but genetic accommodation entrenched differences and supplemented them with morphological adaptations. This process subsequently led to diversification and speciation of the Darwin's finches. Their current behaviour is consistent with this hypothesis as these birds use unusual resources by extraordinary means. In this paper, we identify cognitive capacities on which flexibility and innovation depend. The flexible stem hypothesis predicts that we will find high levels of these capacities in all species of Darwin's finches (not just those using innovative techniques). Here, we test that prediction, and find that while most of our data are in line with the flexible stem hypothesis, some are in tension with it.*

The fauna of the Galápagos Islands is one of the standard examples of evolution's two signatures: diversity and adaptation. There can hardly be a textbook on evolution that does not shelter, somewhere within its pages, a diagram of Darwin's finch beaks showing their divergent functions and morphology. However, morphological variation is not the only readily observed instance of evolutionary change in this species group: the birds illustrate the plasticity of behaviour, too. As we shall see, Darwin's finches have evolved a raft of innovative foraging capacities. However, Galápagos is not just a laboratory of phenotypic evolution. It is also a laboratory of speciation, and in particular of adaptive radiation. 'Darwin's finches' are a poster example of adaptive radiation (Schluter 2000). Fourteen endemic species are now spread over the islands (Grant and Grant 2008) and occupy different niches, but they are one of the few lineages to have diversified. Among the mammals, only the rice rats have diversified, and of the seven reptile lineages that colonized the islands, four have diversified

(Parent et al. 2008). Of the 30 land bird species that are resident on the Galápagos Islands 25 are endemic, but apart from the Darwin's finches only the mockingbirds (*Nesomimus sp.*) have diversified (into four species). Why have just a few Galápagos stem lineages given rise to a crown of distinct species?

In this paper, we assess candidate explanations of the finch radiation. These explanations have a common pattern. All invoke the ecological mosaic—the fragmentation of the habitat into islands—and the special climatic conditions of the Galápagos as central factors in explaining radiation. Many of the islands are subject to severe seasonal and annual fluctuation in rainfall. At irregular intervals they are strongly influenced by the El Niño phenomenon, for the years that follow El Niño events have little or no rainfall, and in these dry years finch populations crash, especially those of low-lying areas (Grant and Grant 1980). The ecological conditions vary from island to island, and the larger islands offer a disparate array of vegetation zones along an altitudinal gradient. Intense intraspecific competition in geographically restricted and fluctuating habitats creates an ecological push for behavioural divergence and the invention of new foraging techniques. Moreover, prior to the adaptive radiation of the initial colonizing species, the complex ecological mosaic of the larger islands was not exploited by a disparate array of species (Grant 1986). If the fauna was low in diversity, then alongside intensively exploited resources there would be those that were rarely or inefficiently exploited. The first tool-using woodpecker finch (*Cactospiza pallida*) was not in competition with woodpeckers, nor the sharp-beaked ground finch with tickbirds. This under-utilization creates an ecological pull, and diverging feeding specializations can then lead to speciation (Morse 1980; Grant 1986).

However, most lineages that arrived at the islands did not radiate. So could ecological fragmentation be a sufficient explanation of finch radiation? Perhaps. As Lewontin (1982) and more recently the niche construction theorists have made clear, the extent to which a landscape is ecologically fragmented does not depend just on the objective features of the physical environment and the extent to which these vary over space and time. It also depends on how a population interacts with its environment (Odling-Smee et al. 2003). The heterogeneity of the Galápagos Islands depends on how the birds experience their world. So perhaps, the islands were ecologically fragmented for the finches, but not, say, for the endemic hawk (*Buteo galapagoensis*), the Galápagos dove (*Zenaida galapagoensis*), or other endemics. So, arguably, the simplest idea in explaining radiation is ecological drive: ecological fragmentation drove finch radiation but not that of other endemics, as only the finches experienced the islands as a set of different habitats. Even this model implicitly presumes that there is something about the finch lineage that explains why they, but not the other small land birds, experience the islands as a set of different habitats.

The distinction between the finch lineage and other endemic birds is not absolute. Also, the mockingbirds have radiated to some degree. They differ in several morphological characters such as plumage colour, size and proportions, but these are minor variations upon a basic mockingbird plan, and they are less pronounced in comparison with the diversity of

the finches (Grant 1986). But the yellow warbler (*Dendroica petechia*), the Galápagos flycatcher (*Myiarchus magnirostris*) and the vermilion flycatcher (*Pyrocephalus rubinus*) did not radiate, although they are small insectivores, like the warbler finch, which is the oldest of the Darwin's finches (Grant and Grant 2008). Likewise, they are songbirds with large brains in relation to their body size (Rehkämper et al. 1991). Prima facie, these birds should also experience the different islands as different habitats, offering different opportunities. There does seem to be something special about the finches.

Two other hypotheses do not deny the central role of the special ecological conditions of the Galápagos Islands, but combine it with some specific feature of the finch lineage; they are two-factor theories of radiation. West-Eberhard (2003) has argued that adaptive radiations depend on individual phenotypic plasticity: they occur when an exceptionally adaptable stem species encounters a new environment. A similar idea (known as behavioural drive) has been defended in Wyles et al. (1983) and Wilson (1985). There is some general evidence that favours a connection between individual flexibility and species richness. Nicolakakis et al. (2003), Sol (2003) and Sol et al. (2005) have recently shown that behavioural flexibility and brain size predict species and subspecies richness in birds. As a measure of flexibility, they used innovation rate, a frequency count of the number of opportunistic, novel or unusual feeding techniques displayed by avian orders and parvorders. In a very recent study, Overington et al. (2009) showed that the diversity of technical innovations in birds explained the greatest proportion of variance in brain size, indicating that innovativeness is related to enhanced cognitive abilities. However, such correlational studies cannot reveal the direction of causation. We will focus on evidence about the finches, in particular, in assessing the argument that behavioural flexibility and innovation has been a driving factor in the evolution and radiation of Darwin's finches (West-Eberhard 2003; Grant and Grant 2008; Price 2008), and compare it with other hypotheses. Some data support the flexible stem hypothesis (FSH), but some are in tension with it.

## The early arrival hypothesis

As noted above, one alternative to the FSH is simply time. Darwin's finches may have arrived earliest, and encountered no competitors (Lack 1947). They had plenty of opportunity to occupy and adapt to different niches. The later arrivals of hawks (Bollmer et al. 2006) and yellow warblers (Browne et al. 2008) are in line with this hypothesis. Moreover, mockingbirds probably arrived at around the same time as Darwin's finches (Arbogast et al. 2006), and they too have diversified, though only into four species. However, the first arrival hypothesis does not explain why the diversification of Darwin's finches was slow at the beginning and rapid only recently, when the environments on the Galápagos Islands changed (Grant and Grant 2008). Grant and Grant (2008) suggest that adaptive radiation of the Darwin's finches was linked with a change in climate and increased habitat diversity. But if the finch radiation was relatively late and triggered by ecological change, we need to explain why late arrivals

like the yellow warbler did not radiate, too. If finch radiation is recent, early arrival drops out as an explanatory factor. It explains radiation only if the early migrants seized the opportunity to occupy vacant niche space before others arrived.

Genetic variability is another potential difference between the finches and the other, less diverse endemics. Darwin's finches show relatively high levels of diversity at the major histocompatibility complex, indicating that ancestral Darwin's finches arrived in a moderately large flock or several smaller ones (Vincek et al. 1996; Grant and Grant 2008). It is therefore conceivable that the evolutionary options of the other endemics were constrained by smaller founder populations. Although possible, it is hard to see how to test this idea (except, perhaps, by comparisons with other island radiations). The FSH is, however, testable, and it will be our main focus.

## The flexible stem hypothesis

In a little more detail, the FSH goes as follows: the foundation populations of the Galápagos endemics were exposed to a novel package of physical stressors, risks and opportunities. In response to this new environment, some birds developed new behaviours: they learned to tolerate unfamiliar substrates while foraging and to exploit new foods which helped them to persist on the inhospitable islands (Grant and Grant 2008; Price 2008). According to this model, initially these changes are not evolutionary: no new genes have appeared and the frequencies of existing genes have not changed since the initial sampling of the founding population. But as time passes and these new environmental conditions persist, selection will change the genetic makeup of the population. For example, on predator-free islands where bolder foraging is advantageous, there will be positive selection for genetic differences that lead some birds to learn that they can afford to be bold more quickly than others. The same will be true of other genetic variants that accentuate, enhance or accelerate adaptive learned responses to the new environment.

In this model then, environmental change results in an initial response mediated by mechanisms of adaptive phenotypic plasticity. But many populations will have relevant pre-existing genetic variation, and sex, recombination and mutation will generate further variation. So, when change persists, there is likely to be some form of genetic accommodation to the new phenotype. The adjustment may be nothing more than a faster and more reliable development of that novel phenotype (as in the Baldwin effect, see Weber and Depew 2003). However, the Baldwin effect is just one special case of genetic accommodation in which the learned response becomes increasingly less dependent on specific experience. Genetic accommodation might also involve enhancing or modifying the response: for example, a change in foraging target may select for modification in beak size or shape, and thus accommodation may involve morphological changes that reinforce behavioural ones. The sharp-beaked finches of Wolf Island may be such a case. Only on this island, finches have learned to drink blood by pecking seabird chicks, and this population has the sharpest and pointiest

beaks (Schluter and Grant 1984; Price 2008).

If West-Eberhard's model is right, individual phenotypic plasticity sets the stage for evolutionary change within the lineage. By this token, we find adaptive radiation in Darwin's finches rather than in other lineages, because individual finches were more adaptable than the members of other founder populations. We must imagine that flexibility allowed finches to respond to environmental variation by adapting differently to different habitats and to the resources available within them. These differences would initially have been merely behavioural, upheld by common mechanisms of learning, but later genetic accommodation would have entrenched some behavioural differences and supplemented them with morphological differences, as morphology co-evolved with behaviour. In this model, differences that are dependent on learning appear first, to be followed by genetic and morphological differentiation and ultimately by isolation and speciation. The model is therefore a version of the 'niche construction' approach to evolution. According to this theory, agents respond to their environment, and in doing so they alter the selective regime. This altered regime then results in further evolutionary change (Odling-Smee et al. 2003; Laland 2008). In this case, learning results in new foraging regimes, which in turn results in selection for genetic variations. This makes the new foraging mode more efficient, more reliably acquired, or both.

## **Innovative foraging in Darwin's finches**

Darwin's finches do seem to be impressively flexible, for the different species show striking capacities for innovative foraging. For example, the woodpecker finch uses twigs or cactus spines to extract arthropods from tree holes (Eibl-Eibesfeldt and Sielman 1962), and an anecdotal observations of this behaviour also exist for the mangrove finch (*Cactospiza heliobatis*) (Curio and Kramer 1964). The sharp-beaked ground finches (*Geospiza difficilis*) are also known as the "vampire finches", because these birds, as noted above, peck at the developing feathers of sea birds, thus drawing blood which they then drink (Bowman and Billeb 1965). Still more impressively, these small birds are able to break the eggs of boobies. These eggs are more than twice as heavy as their attackers (an egg weights around 55 g; the finch only 20 g). To break them, the bird braces its beak against the ground and kicks at the egg with both feet to push it over a ledge or against a rock (Schluter 1984). Two other ground finches, the small ground finch (*Geospiza fuliginosa*) and the large cactus finch (*Geospiza conirostris*), are known to search for invertebrates by using similar methods to move stones, thus exposing arthropods sheltering beneath (DeBenedictis 1966). The small and the medium ground finch (*Geospiza fortis*) glean ticks from iguanas and tortoises (MacFarland and Reeder 1974) and even feed on the afterbirth of sea lions (Grant and Grant 2008). The medium ground finch and large cactus finch capture spiders in the spider's own web by hauling in the silk thread, using a foot to hold each loop (Grant and Grant 2008). Finally, the sharp-beaked ground finch and the small ground finch scavenge on decaying fish, seabird eggs and their dead young, as well as undigested faecal remains from sea birds

(Bowman and Billeb 1965). The only other birds on the Galápagos with similar feeding innovations are the mockingbirds, and they have also diversified. For example, two of the four mockingbird species drink blood from wounded sea lions, iguanas or injured boobies—they may even inflict these wounds on iguanas while removing ticks. Mockingbirds also feed on faecal remains, on the placentas of sea lions and on carrion, and have even been observed to remove morsels from the teeth of sleeping sea lions (Curry and Anderson 1987).

## Genetic assimilation

In the FSH model, the connection between individual adaptive plasticity and lineage-level species richness depends on genetic assimilation entrenching initial divergent responses. This aspect of the model remains speculative, but perhaps plausible for three reasons. First, learning followed by assimilation is an efficient search procedure. A number of novel foraging techniques could arise from relatively simple behavioural modifications of existing practices. Scavenging, feeding on afterbirth and on faecal remains are unusual for passerines, but do not require the invention of new morphologies or behaviours. Likewise, the blood drinking of the sharp-beaked ground finch could be a natural extension of foraging for invertebrates: a misdirected or inadvertently strong peck might well be rewarded with blood, and eventually the accident becomes a habit. Even the use of spider webs in foraging could be attributed to a reinforced accident as many passerines are known to use spider webs in nest construction. It is certainly possible that these one-step changes are the result of a genetic change initiating a new developmental pathway that then leads to a new behaviour. But innovation based on learning followed by reinforcement is more probable than a genetic switch from one hard-wired routine to another, for learning-based exploration searches the local space of foraging options much more efficiently than random mutations (Hinton and Nowlan 1987; Ancel 1999). A population capable of fast trial-and-error learning will explore the space of options more efficiently, for each bird can explore more than one option (Weber and Depew 2003). A behaviour can persist through learning alone, but if the new resources that an innovation secures are both important and lasting, there will be subsequent selection for genetic changes, thus making the acquisition of the new technique more reliable.

Second, some of the more complex foraging novelties of Darwin's finches seem most unlikely to be a single genetic switch away from foraging using only one's own morphology. This is the case with the tool use of woodpecker finches and the egg breaking of sharp-beaked ground finches. Such complex behavioural adaptations, like complex morphological adaptations, are typically assembled one step at a time (Dawkins 1996). Avital (2000) and Jablonka and Lamb (2005) have developed an 'assimilate and stretch' model to explain the evolution of such complex behaviours. In the model, the behaviour under genetic control is a behavioural baseline—a platform upon which learning can build. In an iterative process spanning generations, learning and subsequent genetic assimilation of various components and refinements of the behaviour results in a more complex and adaptively fine-tuned form

of the behaviour.

A potential example of this process can be derived from woodpecker finch tool use. This was first proposed by Bateson (2004) and later by Price (2008). The scenario is as follows. Current tool use is complex: woodpecker finches shorten twigs or cactus spines if they are too long, and have been observed breaking off protruding twigs that would stop the finch inserting the tool into a tree hole. Imagine this tool use as the product of a sequence of slight behavioural and genetic changes which fine-tuned the behaviour over time. At the beginning of the sequence, there was a crude, behaviourally limited form of tool use by which only large, exposed insects could be extracted from shallow crevasses. Proto-woodpecker finches learned by way of an initial innovation, which then spread socially. Once this innovation was common within the population, it was partially genetically assimilated: some aspect of the behaviour, for example, the stabbing motion or the size/weight of the twig to be used, no longer needed to be learned. This promoted faster acquisition of the primitive skill, thus freeing up the cognitive resources to add a further component. Perhaps they learned to select their tool more expertly or learned to shape it. As this component spread and was brought under genetic control, a new baseline competence was available as a platform for further improvement during that period of the bird's ontogeny when it is capable of learning through experimentation. A further improvement might be made, and thus the cycle iterates. Finally, while the scenario above is indeed only a scenario, it fits with what is known of woodpecker finch learning and behaviour. The natural behaviour of the woodpecker finch suggests an underlying iteration of this kind: it is a complex behaviour that seems to have both a genetically fixed component but also components which are developed in ontogeny through individual learning (Tebbich et al. 2001). In an experimental study, Tebbich et al. (2001) investigated intergenerational social learning in these birds by taking six broods from the wild, splitting them, and rearing half of the chicks with a tool-using model and the other half with one that did not use tools. It was found that although trial-and-error learning was important in improving efficiency, both groups learned to use tools. This suggests that the acquisition of tool use depends on a very specific, genetically fixed learning disposition (Tebbich et al. 2001). So while the reliance on genetic assimilation is clearly a speculative component of the FSH, the model does not rely on intrinsically improbable events.

## **Predictions of the flexible stem hypothesis**

The FSH identifies adaptability as the difference between the Darwin's finches and the warbler and the flycatchers. A crucial question, then, is whether we have direct evidence showing that the finches are indeed individually adaptable. Ideally, we would like comparative evidence about the behavioural flexibility of other small Galápagos passerines. We do not have such evidence in these species-poor lineages (apart from novelty responses); however, we can provide data on Darwin's finches, as we have used the finch group as a model system in studying the evolution of behavioural flexibility and its relation to cognition. The West-

Eberhard model predicts a high baseline for learning capacities across the whole Darwin's finch clade and that these are greater than in other comparable groups. However, one might argue that such a high baseline in learning abilities could also be a result of the special selective conditions on the Galápagos and not the legacy of a flexible ancestor. Yet, if the behavioural and cognitive preconditions of innovation are phylogenetically primitive, as the FSH assumes, they should be widely distributed through the crown species and we expect those species with typical foraging practices, not just innovative ones, to be adaptable learners. Thus, we predict that finches without special feeding techniques should be as flexible as those with them, and that they also possess the essential cognitive mechanisms on which these novel techniques depend. These learning capacities need not be identical from species to species: genetic accommodation may have fine-tuned some particular learning trajectory (e.g. increased sensitivity to some particular cue), or it may even have enhanced learning capacities in a specific domain. But the overall learning capacity across the group will be high in comparison to other small generalist birds with fairly short life expectancies. Of course, this test is not decisive. The original difference between the first finches and the other founding lineages might be masked by subsequent evolutionary change, especially as Galápagos lineages have been subject to both strong selection and the effects of small population size, as species suffer population crashes in bad years. Even so, all else being equal, we still expect to see the legacy of ancestral flexibility in living finches.

## **Components of flexibility**

Though the impressive array of finch feeding behaviours provides *prima facie* support for the idea that this lineage is unusual in its behavioural flexibility, this conjecture needs to be tested. However, if we are to measure flexibility, an essential first step is to identify the components from which it is built. We suggest that the following capacities are important components of behavioural flexibility: (i) the seeking of novel information. This includes the willingness to approach novel objects, novel space or novel situations in order to explore them, although responses to new places, objects and individuals do not always covary (Boogert et al. 2006). The underlying mechanism that guides response to novelty is thought to be neophilia—the spontaneous attraction of an animal to a novel item or place (Thorpe 1956). Neophilia has obvious benefits like the discovery of new resources and of new patches of familiar resources or the development of new means of exploiting familiar resources. But it can also incur costs, such as increased risk of predation, and thus neophobia may have evolved to inhibit costly exploration (Greenberg and Mettke-Hofmann 2001). We therefore expect flexible agents to seek novel information particularly in areas where the costs of exploration are low. (ii) To exploit novel opportunities, an agent must be able to learn about the affordances of a new object or situation, typically by some form of operant learning. Thus, we expect fast, effective learning by trial-and-error. (iii) Innovation does not require social learning. Nevertheless, the prospects of successful innovation are improved if

an agent has the ability to learn affordances from others. (iv) In a fluctuating environment, flexible agents should readily react to changes and seek alternative solutions to problems (Bond et al. 2007). Thus, the ability to inhibit previously successful responses is a factor that could enhance flexibility under changing conditions. (v) Agents are most flexible if they can apply what they have learned to a novel situation with the same underlying problem. Underlying mechanisms for this ability can reach from stimulus generalization to insight. It is no coincidence that this list is identical to a list of Reader and Laland (2003) that analyses innovation, for flexibility is a precondition of innovation. Innovativeness can therefore be seen as an indicator of flexibility.

In this paper, we compare innovativeness, exploration, reversal learning and operant learning in Darwin's finches to that of out-group bird species in order to test whether these components of flexibility are comparatively high, as predicted by the flexible stem hypothesis. Additionally, we compare physical cognition between tool-using woodpecker finches and the closely related, but non-tool-using, small tree finches (*Camarhynchus parvulus*). The aim is to investigate whether small tree finches possess some of the cognitive abilities necessary for tool use, for that is what we expect if behavioural flexibility preceded the evolution of this special foraging technique. These data were not collected in order to test these hypotheses, but were analyzed post hoc. Therefore, the evidence is patchy, as the number of species investigated varies and only the woodpecker finch has been studied in detail. However, overall, with some ambiguity, the data are in line with West-Eberhard's conjecture.

## MATERIAL AND METHODS

### Innovativeness

We compared the number of unusual foraging behaviours reported in Darwin's finches (reviewed in Grant and Grant 2008) with the number of feeding innovations reported for new world jays (Overington et al. 2009). Both sources list special typical behaviour and anecdotal observations of unusual or novel foraging techniques and/or feeding substrates. We chose this corvid subfamily because in an analysis of 76 bird families, the corvids were found to have the most diverse innovation repertoire among passerines (Overington et al. 2009). Also, the new world jays have a similar number of genera (7 genera, 38 species) as the Darwin's finches (6 genera, 15 species including the Cocos finch) and like the Darwin's finches are well studied, which reduces biases owing to research efforts.

### Study area, subjects and housing

The laboratory experiments on Darwin's finches were carried out at the Charles Darwin Research Station on Santa Cruz Island in the Galápagos Archipelago, from October 2007 to March 2008 and September 2008 to January 2009. We mist-netted a total of 18 woodpecker

finches, 16 small tree finches and 8 medium ground finches and kept them individually in outdoor aviaries (200 x 100 x 200 cm), which were visually separated. Aviaries were equipped with several natural perches and one experimental platform (40 x 20 x 50 cm), where all experimental set-ups were presented. The operant learning experiments on carrion crows (*Corvus corone*) were conducted by M. Scriba at the Max Planck Institute for Ornithology in Seewiesen, Germany, in August 2009.

## Exploration in a field experiment

The data were collected between January and March 2000. We tested neophilia by placing three novel objects simultaneously in the finches' natural environment at 242 sample points on three different islands (Santa Cruz, Floreana, Genovesa). The objects were one white roller brush (length 14 cm, diameter 6 cm), one black, folded bicycle tube (15 x 7 cm) and a pair of white, flexible plastic tubes (20 x 1.5 cm) bound together with string. We placed the objects on trees 5–7 m and on bushes 1.5–2 m above the ground in areas with low vegetation. We attracted finches by using a bird whistle. After 1 min, the presence of Darwin's finches and other bird species within a radius of 10 m around the objects was recorded. During 10 min trials, we recorded the mean time spent within a radius of 3 m from the object. For each species, we calculated the proportion of individuals present that approached within 3 m of the object during the experiment.

However, calculating this proportion per sample point would often result in the value 0 or 1 because at many sample points, only one individual per species was present at the start of the experiment. We therefore pooled the data from all sample points and calculated (per species) the ratio between the total number of individuals approaching within 3 m and the total number of individuals present within 10 m. This resulted in a single percentage-value per species and island. For further details, see Tebbich et al. (2009).

## Operant learning

The 18 woodpecker finches, eight small tree finches, eight medium ground finches and eight carrion crows were presented with a box (3 x 2 x 2.3 cm for Darwin's finches and 10 x 14 x 13 cm for crows) containing a food reward. The box was closed on top with a hinged, transparent Perspex lid which overlapped one edge of the box. In order to obtain the food reward, birds had to push open the lid. They were tested twice a day and in a maximum of six experimental sessions, each lasting 25 min. We measured success or failure to open the box and how many trials were needed to success.

## Reversal learning

In this task, individuals were first trained in a discrimination task. Once they had learnt this discrimination, the reward contingencies were reversed. The test apparatus consisted of two white boxes (each 3 x 2 x 2.3 cm) that were mounted 10 cm apart on a wooden base (20 x 20 cm) and covered with coloured foam lids. A Perspex divider (29.5 x 21 cm) between the boxes prevented the birds from removing the lid of the second feeder once they had made their initial decision. First, birds were trained to remove the lids. In the initial discrimination task, the 16 woodpecker finches, eight small tree finches and eight medium ground finches had to learn that of the two feeders with different coloured lids (blue and orange), only one was rewarded. Once they had learned this colour–reward relationship, they moved on to the reversal phase in which the learning rule was reversed. Half of the birds were first rewarded with orange and the other with blue. We measured the number of trials needed and the number of errors made in attaining criterion (see below). We compared our data with the original data of a comparative study of Bond et al. (2007) (Table 4.1). In this study, five pinyon jays (*Gymnorhinus cyanocephalus*), five western scrub jays (*Aphelocoma californica*) and five Clark’s nutcrackers (*Nucifraga columbiana*) were first trained in a skinner box to gain a food reward by pecking a coloured, illuminated key. In the discrimination and reversal procedure, they had to peck three times at one of two illuminated side keys (red or green) in order to obtain a food reward. For further details, see Bond et al. (2007). We also present data on reversal learning from a study on pigeons (*Columba livia*) by Lissek et al. (2002) (Table 4.1), but did not include them in the statistical comparison because we could not obtain the original data. Like the corvids, the pigeons were tested in a skinner box. The pigeons had to peck once at one of two illuminated keys to gain 3 s access to food. The criterion to success was 15 correct in a row.

## Cane task

This test involved making a choice between two canes (12 cm apart), each with a food reward placed either on the outside or the inside of the hook (Figure 1.2a, Chapter 1). Only pulling the cane with the food reward in line with its concave portion was rewarded. The canes rested on a rectangular base (15 x 24 x 1 cm) which was covered with a low, transparent Perspex lid that was open at the front. Twelve woodpecker finches and six small tree finches were tested. The bird could see the configuration from above but could only gain access to the food once it had been pulled out from underneath the lid. The two canes were connected by a string, so pulling one cane caused the other to simultaneously withdraw into the apparatus. Thus, if one cane was pulled past a certain point, the decision was irreversible. Individuals that reached significance in the initial cane task were tested in a series of transfer tasks. These were variations of the initial task configuration that were designed to investigate stepwise how well the birds transferred their knowledge of the importance of contact to fur-

ther configurations (Figure 1.2b–e).

## Seesaw task

A seesaw platform was presented surrounded by a transparent box (Figure 1.1a, Chapter 1). Perching on one of the two levers tilted the seesaw towards the subject and caused the reward to roll towards it. During training, the seesaw platform was continuous, while for testing the surface was interrupted by a hole that was placed either centrally (Figure 1.1b) or 2.5 cm off-centre (Figure 1.1a). In order to obtain the reward, the bird had to hop onto the lever that caused the food to roll down the continuous portion of the seesaw surface and out of the apparatus. Twelve woodpecker finches and six small tree finches were tested. Half the birds received the gap-central condition while the other half received the food-central condition. In the transfer task, the birds were presented with the alternative condition (Figure 1.1b).

## Criterion and testing procedure for reversal learning, seesaw task and cane task

Individuals were tested daily in two sessions of 10 trials in which the correct side was pseudo-randomized and counterbalanced right and left, so that there were five trials in each position per session. The number of trials in which the reward was presented consecutively on one side never exceeded three, except in the case of a side bias correction procedure (see below). The birds were given a maximum of 140 trials in the discrimination/reversal-learning task, up to 160 trials in the seesaw task, up to 150 in the cane task and up to 30 trials in the cane transfer tasks. The criterion for passing a test was seven consecutive correct trials or at least 8/10 correct trials in two consecutive sessions or in one session all 10 correct. In the comparative study on corvids (Bond et al. 2007), the birds received one block of 36 trials a day and in contrast to our study no correction trials for side biases (see below). The criterion for success in the discrimination and subsequent reversal was 90 percent correct in three successive sessions of 36 trials. To make the data more comparable, we only included the number of sessions required to first achieve 90 percent correct. Nevertheless, we cannot entirely exclude overtraining in the corvids as a factor in their slower reversal learning. In the comparative study on pigeons (Lissek et al. 2002), acquisition and reversal session lasted until the learning criterion of 15 correct responses in a row was reached, with session duration not to exceed 3 h. Like the corvids, the pigeons received no correction trials for side biases.

## Correction procedure

If a bird developed a side bias, defined as six consecutive choices of one side during one session or over two sessions, in subsequent trials the reward was only presented on the non-preferred side until the subject chose that side and was rewarded. At that point, we reverted

back to the original randomized trial configuration. In the analysis, the correction trials were not treated differently from non-corrected trials.

## Statistical methods

An extension of the Fisher's exact probability test to 2-by-K contingency tables (R x C-exact-test) was used to test the species difference in number of individuals that reached the criterion in the operant task, the seesaw task and the cane task as this test can be used with small sample sizes, sparse, imbalanced or heavily tied data (Fung and Lee 1989). Species differences in exploration, the number of trials to reach criterion in the cane task, and post hoc comparison were assessed with Mann–Whitney U-test. To test for differences within Darwin's finches and between species groups in reversal learning, we used an analysis of variance (ANOVA).

## RESULTS

### Innovativeness

In order to test whether Darwin's finches are indeed exceptionally innovative, we compared the number of unusual foraging behaviours reported in Darwin's finches with the number of feeding innovations reported in new world jays, which belong to an exceptionally innovative bird family (Overington et al. 2009). As predicted by the FSH, Darwin's finches had a significantly higher number of feeding innovations per species (median=1, range 0–8) than the new world jays (median = 0, range 0–9; Mann–Whitney U-test:  $U = 183.5, p = 0.011$ ).

### Exploration

In a nearly predator-free environment like Galápagos, the costs of exploration are low and we therefore expect little fear of novel situations (neophobia). Investment in exploration by Darwin's finches and the other terrestrial Galápagos bird species may depend only on the variable benefits of seeking novel information (neophilia). The FSH would therefore predict that Darwin's finches are more neophilic than other Galápagos bird species. In order to test this prediction, we compared the reaction to novel objects of Darwin's finches with that of five other bird species from Galápagos in a field experiment. The comparison did not support our prediction: we found no significant difference between Darwin's finches and other Galápagos birds species in terms of the percentage of individuals that approached the novel object to within 3 m (Darwin's finches: median percent = 39.5, range = 11.1–67.6; other bird species: median = 44, range = 41.1–72.3; Mann–Whitney U-test:  $U = 16, p = 0.117$ ).

## Reversal learning: learning to inhibit a previously learned response

Reversal learning has been used to investigate behavioural flexibility in animals and humans. In this experiment, flexibility is measured by the speed with which subjects learn that a previously successful strategy is no longer rewarded. We found no significant differences between woodpecker finches, small tree finches and medium ground finches in the initial discrimination phase (Table 4.1; ANOVA:  $F_{2,29} = 2.508$ ,  $p = 0.099$ ). In the subsequent reversal task, we found no significant difference in the number of trials that the three species needed to reach the criterion (ANOVA:  $F_{2,29} = 1.207$ ,  $p = 0.314$ ). However, woodpecker finches did make significantly more errors than the small tree finches in attaining criterion in the reversal task (Mann–Whitney U-test:  $U = 28.00$ ,  $p = 0.027$ ). We attribute this to their extractive mode of foraging. Extractive foraging requires perseverance, and perseverance in turn requires that an agent continues with a behaviour even when it is not rewarded. Fast reversal learning requires just the opposite.

Comparative data from other bird species indicate that these three Darwin's finch species are indeed unusually fast reversal learners. Unfortunately, no comparative data are available from small short-lived passerine species with a similar ecology. However, comparable data on visual discrimination and reversal learning are available from pigeons (Lissek et al. 2002) and three species of corvids (Bond et al. 2007) (Table 4.1). The corvid data are of special significance as corvids are large-brained birds, known for their feeding innovations and their extraordinary cognitive abilities across various domains (Emery and Clayton 2004).

**Table 4.1** Mean number of trials and mean number of errors (with S.E.M.) needed to reach a significant criterion in the acquisition and reversal phases of a visual discrimination task with pigeons, three corvid species and three species of Darwin's finches.

species	N	acquis.	S.E.M.	reversal trials	S.E.M.	reversal errors	S.E.M.
pigeon <i>C. livia</i>	8	40		168		99	
<b>corvid species</b>							
pinyon jay <i>G. cyanocephalus</i>	5	149.6	33.6	155.0	28.3		
western scrub jay <i>A. californica</i>	5	136.8	20.9	191.0	35.7		
Clark's nutcracker <i>N. columbiana</i>	5	122.4	8.18	142.6	3.6		
<b>Darwin's finch species</b>							
small tree finch <i>C. parvulus</i>	8	41.1	18.4	76.3	13.8	37.4	6.8
woodpecker finch <i>C. pallida</i>	16	39.8	2.7	95.6	5.4	56.4	4.8
medium ground finch <i>G. fortis</i>	8	56.1	9.2	93.7	12.5	46.4	7.9

Nevertheless, they took significantly more trials to reach criterion in the reversal phase of a comparable visual discrimination task (ANOVA:  $F_{1,46} = 31.9, p = 0.001$ ). It is, however, possible that the speed of learning might be slower for animals tested in an operant box than for those tested in our experimental set-up. Furthermore, the three corvid species were not corrected for any side biases. Both factors could have affected the speed of learning in corvids but are unlikely to account for the substantial difference between the two groups.

## Operant learning

The ability to solve a novel operant task differed significantly between the four tested species (R x C-exact-test:  $\chi^2 = 7.94, p = 0.04$ ). Forty-four percent of the woodpecker finches and 62.5 percent of the carrion crows were able to open a novel box with a transparent lid while none of the small tree finches and only 25 percent of the medium ground finches managed to do this in six experimental sessions (post hoc comparisons R x C-exact-test: woodpecker finches versus small tree finches,  $\chi^2 = 5.13, p = 0.03$ ; carrion crows versus small tree finches,  $\chi^2 = 7.23, p = 0.02$ ; all other comparisons n.s.). The difference between the woodpecker finch and small tree finches can again, as in the reversal task, be attributed to the perseverance of woodpecker finches. Woodpecker finches made more contacts proportional to time tested (median = 2.3, range = 1.0–25.2) than small tree finches (median = 1.3, range = 0.7–2.9; Mann–Whitney U-test:  $U = 28, p = 0.013$ ).

These results show that the performance of woodpecker finches and medium tree finches in this operant task is similar to large brained corvids but also that problem-solving can be influenced by other factors such as persistence. Further evidence showing that woodpecker finches are fast trial-and-error learners comes from a comparative study in which woodpecker finches performed similarly to primates in series of problem-solving tasks (Tebbich and Bshary 2004).

## Physical cognition in tool-using and non-tool-using finches

It is not surprising that species with complex and distinctive but species-typical behavioural adaptations, like tool use, have evolved specific cognitive or learning strategies, as these explain the reliable acquisition of such unique foraging skills. However, according to the FSH, we also expect finches without these complex foraging routines to show a high learning baseline. One important line of experimental research supports this prediction: we ran a series of experiments to compare the physical cognitive learning abilities of woodpecker finches and small tree finches and found no major difference in physical intelligence among these species.

## Cane task

In the cane pulling task, there was no difference in the speed with which woodpecker finches (median trials to success = 116.5, range = 70–149,  $N = 8$ ) and small tree finches (median trials to success = 106.5, range = 76–140,  $N = 6$ ) learned to choose the correct configuration (Mann–Whitney U-test:  $U = 19$ ;  $p = 0.573$ ) nor was there a significant difference in the number of individuals of each species to attain criterion in the initial task (woodpecker finches eight of 12 and all small tree finches,  $R \times C$ -exact-test:  $\chi^2 = 3.462$ ,  $p = 0.11$ ). Moreover, three small tree finches and six woodpecker finches were able to transfer their acquired knowledge to slightly different tasks (Figure 1.5b-c).

## Seesaw task

Individuals from both species were able to solve the seesaw task, but small tree finches outperformed woodpecker finches: five of six small tree finches solved the initial task, but only two of 12 woodpecker finches ( $R \times C$ -exact-test:  $\chi^2 = 7.481$ ,  $p = 0.012$ ). None of the tested birds passed the transfer task. These results, showing little difference in physical cognitive intelligence between woodpecker finches and small tree finches, indicate that the capacities shared by the clade have been co-opted for the specific woodpecker finch niche—a finding which is consistent with the FSH. The results are inconsistent with the alternative hypothesis, namely the capacity to solve physical problems evolved in the woodpecker finch in response to a specific ecological challenge.

## A BRIEF CONCLUSION

Tebbich's and Teschke's experiments were not designed to test the flexible stem hypothesis, but rather to test hypotheses about the relationship between adaptive behaviour and cognitive mechanisms. Nevertheless, some of our results are in line with the FSH: we found that the Darwin's finch species show a high baseline in behavioural parameters that are plausible components of flexibility (i.e. reversal learning, operant learning and reported innovation rate). In these abilities, they rival and even outperform large-brained corvids. We also found that small tree finches, a close relative of the tool-using woodpecker finches, seem to possess the cognitive foundations for tool use, which is in line with the idea that the preconditions of innovation are phylogenetically primitive. The data on exploration are in tension with the FSH: Darwin's finches were not more apt to explore than four other Galápagos bird species. We are aware that our data only provide preliminary evidence. A full test of the FSH would at the very least require the following:

- The development of a more nuanced and empirically tractable breakdown of the cognitive and behavioural capacities underlying flexibility and innovation. To

more exhaustively test the FSH, we need to compare birds across a wide range of cognitive dimensions, and not just a few.

- Extensive knowledge of the ontogeny of other special feeding techniques in Darwin's finches. The ontogeny of a capacity is clearly relevant to its potential for development, redeployment and recombination with other elements of an animal's repertoire. As with other aspects of an agent's phenotype, the more modular a skill, the more freedom it has to vary independently of the rest of the agent's repertoire (Lewontin 1978), and the more it is a potential site of innovation. More knowledge in this area would allow a more competent assessment of the role of special feeding techniques in the evolution and adaptive radiation of Darwin's finches.
- Most obviously, we need a broader comparative base across the finch species, between the finch species and mockingbirds, and between these two diverse lineages and those endemics that have not diversified. Only a full comparative test can tell us whether: (i) the finches collectively are more behaviourally flexible than other endemics and (ii) whether standard-model finches are as flexible as those with novel foraging methods.

Almost all scientific papers end with a clichéd remark on the need for further research. In this case, it is no cliché. That said, the FSH makes two central predictions: (i) the finches are more flexible than the endemics that did not radiate and (ii) flexibility in the finches is primitive; it preceded rather than evolved with innovation. The bottom line is that while we have very little data on the first prediction, the little that we have does not confirm it. We have much more data on the second, and this is confirmed.

## ACKNOWLEDGEMENTS

We thank the Galápagos National Park Service and the Charles Darwin Research Station, especially S. Cisneros, P. Couenberg and B. Fessl, for logistic support. We would also like to thank S. Stankewitz, E. Cartmill, P. Buitron Lopez, T. Quisingo Chiza, M. Jaramillo, V. Morales, P. Meidl and C. Raby for data collection and field assistance. E. Cartmill helped with the design of the seesaw task. C. Neuner and O. Fraser provided statistical advice. We are grateful to A. Bond and M. Scriba for providing original data. We thank M. West-Eberhard for brief comments and two anonymous referees for their constructive suggestions. S.T. is funded by the FWF (project number V95-B17) and I.T. by the DFG (project number TE 628/1-1). The University of St Andrews provided additional funding for materials and travel. All research carried out on Darwin's finches adhered to Ecuadorian laws and was approved by the Galápagos National Park.



## GENERAL DISCUSSION

---

The primary goal of my doctoral work was to contribute to our understanding of the evolutionary link between cognition and tool-use in the woodpecker finch. More specifically, I wanted to know whether this species is predisposed either through experience or genetic composition, to learn about certain kinds of information that are relevant to their natural tool-use. Finally, I also hoped to improve our comprehension of the evolutionary history of tool-use in this species.

I believe that this work has brought us a step forward in these areas, though many questions concerning the evolution of tool-use in this species remain open. In this final section of my thesis, I review my major findings, their implications and the future avenues of research.

### MAIN FINDINGS

Since the first question (Chapters 1-2) was also the starting point of my thesis while the remaining investigations (Chapters 3-4) arose from this primary question, I will begin by describing my main findings regarding Question 1.

*Did specialized cognitive abilities involving sensitivity to physical interactions evolve in conjunction with tool-use in woodpecker finches (*Cactospiza pallida*), a tool-using Darwin's finch species?*

In Chapters 1 and 2, I set out first and foremost to find out whether woodpecker finches, a tool-using Darwin's finch species, exhibit enhanced cognitive abilities pertaining to the physical interactions governing tool-use. Furthermore, the fact that there are woodpecker finches that have tool-using experience and those that do not, made it possible to tease apart cognitive qualities that develop through tool-using experience from those that can be attributed to the genetic composition of a tool-user. I tested this tool-using species and a comparable, closely related non-tool-using species in a battery of tasks designed to pinpoint

subject's sensitivity to various aspects of the physical world including surface continuity (Seesaw task: Chapter 1, Experiment 2), the functional spatial relationship between tool and reward (Cane task: Chapter 1, Experiment 3) and general physical interactions (Two-trap tube task: Chapter 2, all experiments). Woodpecker finches did not excel in any of these three tasks compared with small tree finches (*Camarhynchus parvulus*). Thus, the investigations presented in the first two chapters provide no evidence that woodpecker finches have a more sophisticated understanding of physical interactions involved in these physical tasks than small tree finches. Though the tool-use of woodpecker finches has been shown to involve some degree of task-specific modification and selectivity (Tebbich and Bshary 2004), this must not necessarily be associated with sophisticated cognition, rather there appear to be simpler cognitive routes which are capable of producing successful and seemingly complex tool-use. One tool-using woodpecker finch applied a strategy in the cane task that was successful in multiple versions of the original problem. This exemplifies how a simple trial-and-error strategy—in this case monitoring the effect of one's own actions on events—can go a long way even in a range of varying situations.

Unsurprisingly, at least some individuals of both species were able to attend to simple perceptual cues in forming predictive rules during the initial learning phase of most of the physical tasks. Indeed, small tree finches seemed particularly good at this: in the initial seesaw task, significantly more small tree finches than woodpecker finches were able to make use of such information and small tree finches also outperformed non-tool-using woodpecker finches in the initial phase of the cane task. Nevertheless, it is important to understand that success in the initial learning phase is not suggestive of an advanced physical cognitive ability, rather it simply indicates attendance to some perceptual cue that reliably predicted success.

Given this, the low number of individuals that were successful in the initial phases of the seesaw and trap tube tasks is somewhat troubling. In particular the two-trap tube task with the pre-inserted stick (Chapter 2, Experiment 2) apparently posed substantial difficulties to the birds: only 2 of 12 woodpecker finches and no small tree finches were able to solve the initial phase of this task. Ideally, all birds would have been successful in learning the initial task at least by using some simple perceptual cue if not via a more complex rule. The generality of the learned rule would then have materialized in the transfer situations that test how widely applicable the learned rule is in a variety of situations. The fact that only a low number of individuals solved the initial tasks hints that there might have been features of the task that were confusing or distracting to the birds. In the future, simpler designs which all birds can solve at least initially using simple perceptual cues, should be used. One alternative to the trap tube task with a pre-inserted stick is the design used by Liedtke et al. (2010) which allows direct movement of the food with the beak.

The comparisons of general learning abilities could help to understand the small tree finches' enhanced ability to attend to simple predictive perceptual cues in a variety of settings. Small tree finches outperformed woodpecker finches in reversal learning, a measure

for flexibility in associatively learned rules though woodpecker finches performed better in a novel operant task where perseverance and the application of an extensive repertoire of motor behaviours presumably were the main factors leading to success. The enhanced reversal learning ability of small tree finches could be due to enhanced flexibility in re-learning rules and also might be the reason that small tree finches were able to learn so well about predictive cues in the other tasks. This species difference in flexibility combined with the finding that woodpecker finches were better at the task requiring perseverance, lead us to the idea that the perseverance involved in the long bouts of pecking which woodpecker finches often engage in during extractive foraging (but not necessarily during tool-use), could impede learning flexibility. This was the next major line of inquiry that I pursued in my thesis and the experiments designed to test this hypothesis are described in Chapter 3.

*Is perseverance arising from woodpecker finches' persistent foraging ecology, linked to an impaired flexibility in learning simple associative rules? How is a consistent reaction to novelty related to reversal learning performance?*

In the next investigation, I used two new reversal conditions that were specifically devised to pinpoint whether woodpecker finches are more susceptible to persevering in choosing a cue which they associate strongly with a reward than small tree finches. However, testing with the new reversal learning paradigms yielded no evidence to support this hypothesis.

Another line of questioning which I pursued in this investigation was the possibility that there might be a difference in novelty response between species that could also be related to learning abilities. We found that individuals were consistent in their relative levels of individual neophobia. Furthermore, woodpecker finches were significantly less neophobic than small tree finches though there was no significant difference between species in neophilia. Finally, we were able to find some indication that reversal learning performance correlated negatively with neophobia for woodpecker finches but not for small tree finches. More specifically, those woodpecker finches that were most neophobic also made less proportional errors in the reversal phase of the classical reversal learning task and also those that were most neophobic learned the reversal phases of both of the new reversal conditions (LNR and P) more quickly. This draws attention to a main issue in cognitive psychology, namely that cognitive abilities are very often linked to the properties of other cognitive mechanisms such as memory, perceptual abilities, attention and motor-skills.

*What is the evidence for and against the hypothesis that the ancestors of all Darwin's finches shared certain cognitive mechanisms (high trial-error-learning ability, explorative tendency, flexibility) that led to their relatively rapid and extensive diversification?*

While Chapters 1 and 2, are concerned with the hypothesis that tool-use evolved in conjunction with certain cognitive abilities and Chapter 3 with the investigation of a question stemming from Chapter 1, the last chapter of my thesis is concerned with a scenario in which ancestral cognitive characteristics of the Darwin's finch clade might have driven the evolution of woodpecker finch tool-use.

The flexible stem hypothesis (FSH) proposes behavioural flexibility as a key factor driv-

ing the speed and scope of adaptive radiation because it results in an increased capacity to invade new habitats and subsequent exposure to new selection pressures (West-Eberhard 2003). The surprising degree of Darwin's finch diversification in a relatively short period of time ( $\leq 3$  million years) compared with other Galápagos lineages hints that this clade might have descended from a flexible stem species: they are the only Galápagos clade to have radiated so extensively [Mockingbirds (*Nesomimus sp.*) also radiated on the Galápagos but only into 4 species] and this is not entirely explained by an earlier arrival on the islands compared to other endemics.

We propose that an unusual ability to inhibit previously learned responses (reversal learning), a high tendency to seek novelty, quick trial-and-error learning, and a high innovation rate are the predicted characteristics of the crown species of a flexible stem lineage. Using our own data along with comparable data gathered from the literature, we tested these predictions derived from the FSH. We expressly tested whether these characteristics are present in Darwin's finches to an unusual degree compared with other unrelated Galápagos passerines (only in terms of exploration) and also compared their abilities to those of corvids, an avian group that is already known to be highly innovative and to possess at least some of these characteristics in comparatively high measure.

Several pieces of evidence supporting the FSH for Darwin's finches were unearthed. It turned out that Darwin's finches might be similarly flexible compared to some corvids in associative rule-learning and also that they exhibit significantly more unusual feeding innovations per species than new world jays, a corvid group well-known for its innovative capacity. Furthermore, 2 of 3 Darwin's finch species performed similarly to corvids in a trial-and-error problem. However, other unknown factors such as perseverance might have played a role in solving the task and prevent a clear interpretation of the significance of this result for the FSH. Finally, the findings of Chapter 1 and 2, namely that non-tool-using small tree finches and closely related woodpecker finches share similar cognitive abilities—if anything, small tree finches seem more adept at learning simple associative rules—hints that the cognitive qualities that facilitated the evolution of tool-use in woodpecker finches are phylogenetically primitive.

On the other hand, contrary to the FSH predictions for Darwin's finches there was not any indication that members of this group are not more novelty seeking (neophilic) than other Galápagos bird species. In summary, we were able to provide some experimental evidence in support of a remarkably flexible and adaptable Darwin's finch stem species, but this evidence is not incontrovertible. Further experiments might lend more evidence supporting the credibility of this hypothesis for Darwin's finches.

## IMPLICATIONS

Perhaps most importantly, instead of establishing that tool-use acted as a prime driving factor of cognition in this species, I instead found the opposite, namely that certain cognitive abilities might have been present prior to the evolution of tool-use and paved the way for its development. This is timely and complements the recent findings of Bird and Emery (2009) regarding the evolution of cognition and tool-use in corvids. In their study, rooks, a non-tool-using corvid species that had been trained to use tools, were able to modify tools appropriately to a task at hand, demonstrated remarkable selectivity based on the functional features of tools, and even displayed creative tool manufacture using a novel material in a manner rivaling that of tool-using New Caledonian crows. The authors interpret their findings as evidence that the necessary cognitive abilities for tool-use are ancestral in corvids and that the tool-use of New Caledonian crows is more likely a “useful by-product” of cognitive abilities that evolved in another context rather than a driver of intelligence (Bird and Emery 2009, p.5). Combined, Bird and Emery’s findings for corvids and my findings for woodpecker finches impact the way that we understand the evolution of tool-related cognition in animals: while it was previously thought likely that tool-use is a driving force behind cognitive abilities, we now have two convergent cases of tool-use in which it appears that the directionality is reversed.

Having said this, it must be acknowledged that the dynamics involved in the evolution of tool-use are almost certainly more complex than the “either/or” scenarios mentioned above. Flexibility might have formed the cognitive foundation for tool-use, however it is still possible that tool-use did hone some aspects of cognition. I necessarily tested only a subset of cognitive abilities—the ones I thought most likely to be associated with tool-use in this species—but not all abilities were tested nor did I undertake a comparative investigation of the ontogeny of tool-related cognition. Thus, I cannot exclude the possibility that some aspect of physical or general cognition was enhanced in woodpecker finches in conjunction with tool-use. For the moment at least, it appears that the non-stereotyped tool-using behaviour of woodpecker finches is achieved via simple learning mechanisms which nevertheless generates a degree of flexibility.

It is worth emphasizing that though both Darwin’s finches and corvids apparently are unusually flexible and innovative groups, the level of cognition which we postulate for Darwin’s finches is on a low level compared to that of corvids. This is best illustrated by comparison of their trap tube performance: while no Darwin’s finches were able to learn anything else about this task but simple perceptual rules that only worked in one specific situation, corvids learned general rules that could be transferred to a number of situations (Seed et al. 2006; Taylor et al. 2009). Being able to make such cross-species comparisons is one of the major advantages of using comparable paradigms for distantly related animals.

The last chapter of my thesis has moved us forward in our understanding of the evolution of Darwin’s finches more generally. Our test of the FSH is only a preliminary attempt

to test the relevance of this idea for Darwin's finches. Nevertheless, using data that was not collected for the purpose of testing this hypothesis still afforded some thought-provoking evidence in support of the FSH. This paves the way for more rigorous studies of the hypothesis for Darwin's finches in the future.

The results of my thesis combined with what is already known about the adaptive value of tool-use in woodpecker finches, its ontogenetic development and associated cognitive abilities moves us towards a more complete understanding of tool-use in this species. It highlights the importance of devoting resources to understanding not only the proximate aspects of animal tool-use but also to understanding its survival value and evolutionary history.

## FUTURE DIRECTIONS

This shift in our understanding of the role of tool-use in cognitive evolution underlines the importance of employing controlled two-species comparisons to evaluate shared ancestry as an explanation for the evolution of cognitive abilities or remarkable behaviours. The search for divergence in closely related species is a course that is often overseen in evolutionary studies of cognition in favour of the search for convergence in distantly related species. In light of the benefits that this approach has afforded to our understanding of the evolution of tool-use in woodpecker finches, I hope that this method will be used more often in future studies of animal cognition.

Further investigations of specialized cognition should avoid complicated paradigms like the trap tube since there is much disagreement about what cognitive processes are actually involved in solving it. On the other hand, the advantage of the trap tube is that there is much comparative data available. In the future, it would be helpful to develop paradigms that are well-defined and then seek to test a wide range of species with them.

Though we understand more about the mechanisms, evolution and ontogeny of woodpecker finch tool-use than ever before, we still cannot provide a satisfying answer to the tantalizingly simple question: "why do woodpecker finches use tools while small tree finches do not?". In further attempts to answer this question, the details of the information processing underlying woodpecker finch tool-use will continue to be an interesting avenue of research. Thereby, simpler paradigms must be found and there should continue to be a strong focus on the woodpecker finches' natural tool-using ecology in generating new hypotheses about the types of information which should be most relevant in their natural tool-use. It would be particularly important to find out more about the cognitive abilities and characteristics which facilitate the ontogenetic development of tool-use in woodpecker finches. Central questions in this area are: what are the specific environmental cues that trigger the development of tool-use in woodpecker finches? And how do woodpecker finches compare with small tree finches in terms of their tendency to manipulate objects and in exploration throughout ontogeny?

At the moment, we know next to nothing about the neurobiology of these particular tool-users. Recently, Mehldorn et al. (2010) demonstrated that brain areas of New Caledonian crows which are linked to association and motor-learning, are enlarged compared to other corvids and sparrows. Woodpecker finches are also prolific tool-users and therefore it would be interesting to see whether Mehldorn et al.'s findings for New Caledonian crows might also hold for woodpecker finches. Furthermore, it might be worth looking at neural substrate associated with flexibility and compare this in Darwin's finches and an outgroup. This would be useful in establishing which characteristics of the ancestral Darwin's finch species were different from its mainland relatives. More generally, such information in addition to other data on more species of Darwin's finches and other Galápagos passerines are needed to conduct a more robust test of the FSH for Darwin's finches.

There are still many exciting questions about animal tool-use and more generally within the field of cognitive psychology that are waiting to be answered. Though some problems are so daunting that many of us cannot envision that a solution will ever be found, I believe that the majority of challenges are within our reach. It is my hope that unconventional approaches to studying cognition coupled with technological innovation and a strong curiosity directed towards all levels of behaviour will eventually overcome the obstacles placed in our way. If not, at least we will go a long way towards understanding animal cognition in the process of trying to find answers to our questions.



## SUMMARY

---

Tool-use in the animal kingdom is more common than previously believed. The cognition associated with this remarkable behaviour and the evolutionary dynamics between cognition and tool-use remain a mystery in the case of most animal tool-users. In my thesis, I set out to investigate the cognitive evolution of a tool-using bird species, the woodpecker finch (*Cactospiza pallida*). This species belongs to the Darwin's finch clade and is renowned for its use of cactus spines or twigs in extractive foraging. Despite the finding that woodpecker finches have a strong genetic propensity to develop functional tool-use during ontogeny, laboratory studies have shown that adult tool-use is nevertheless characterized by modification to a task at hand and selectivity. This, in combination with the high survival value of woodpecker finch tool-use, leads to the expectation that cognition might have co-evolved with tool-use to improve the development of this behaviour and/or tool-deployment in this species.

In my thesis, I asked specifically whether tool-use evolved in conjunction with enhanced cognitive abilities in woodpecker finches, and if so, whether these cognitive adaptive specializations are restricted to the domain of tool-use or rather are more general cognitive adaptations. I was also interested in examining potential pre-conditions that might have facilitated the evolution of this unusual behaviour.

In Chapter 1, I compared the performance of tool-using woodpecker finches with a closely related non-tool-using species, the small tree finch (*Camarhynchus parvulus*) in general learning tasks (reversal learning and novel problem-solving) and in two tests of tool-related physical cognition. Physical cognition refers to the ability to use physical forces and related events in the environment to form general rules. In Chapter 2, I extended this comparison by testing a further aspect of physical cognition—the appreciation of general physical interactions in a physical problem—using a widespread paradigm, the trap tube.

I found no evidence supporting an enhancement of physical cognitive abilities in woodpecker finches. Indeed, the high flexibility of small tree finches in the reversal learning task and their proficient performance in the physical tasks suggests that the cognitive abilities necessary for woodpecker finch tool-use might have preceded the evolution of this behaviour, an idea that is addressed further in Chapter 4. Though tool-users were less flexible in reversal learning, they were more successful in a novel operant task.

Chapter 3 utilizes two modified reversal regimes to examine the hypothesis that the deficit in reversal learning in woodpecker finches (Chapter 1) might be a trade-off linked to the extractive foraging mode of this species: besides using tools, they are often seen to engage in long bouts of pecking to extract cryptic prey from a substrate. This perseveration is surely useful in extracting prey, but might also lead to a relatively low sensitivity to a change in reward contingency. Here, I also looked at the role of novelty reactions in reversal learning and compared novelty reactions between species.

Species differed in neophobia, but not neophilia, with woodpecker finches being less fearful of new objects than small tree finches. I could not confirm that woodpecker finches' impaired flexibility was due to an inability to inhibit a previously learned positive association. Interestingly, some of the findings from Chapter 3 tentatively suggest that slow explorers might be faster at reversal learning but an investigation of the relationship between novelty reactions and learning in the new reversal conditions could not provide an explanation for this finding.

In the last chapter (Chapter 4), tool-use plays a supporting role as a manifestation of cognition that might have preceded and facilitated the evolution of such a feeding innovations amongst Darwin's finches. Here, I review evidence relevant to the idea that a highly flexible stem species of Darwin's finches might explain their rapid and extensive radiation. The strongest support for this hypothesis came from the high flexibility of Darwin's finches, as demonstrated by their proficiency in reversal learning performance, even compared to other innovative species, and also the high number of unusual feeding adaptations in Darwin's finches. However, other findings such as the lack of difference in exploration between Darwin's finches and other Galápagos passerines that did not radiate, are not in accord with this hypothesis.

The results of my thesis combined with what is already known about the adaptive value of tool-use in woodpecker finches, its ontogenetical development and associated cognitive abilities moves us towards a more complete understanding of tool-use in this species. It highlights the importance of devoting resources to investigating not only the proximate aspects of animal tool-use but also to appreciating this striking behaviour in an evolutionary context.

# ZUSAMMENFASSUNG

---

Werkzeuggebrauch ist weiter im Tierreich verbreitet als bisher angenommen. Die kognitiven Fähigkeiten, die mit diesem bemerkenswerten Verhalten verbunden sind, sind weitgehend unerforscht, ebenso wie die evolutionäre Dynamik zwischen Kognition und Werkzeuggebrauch. In meiner Dissertation beginne ich, die kognitive Evolution einer werkzeuggebrauchenden Vogelart zu erforschen, des Spechtfinken (*Cactospiza pallida*). Diese Art gehört zur Gruppe der Darwinfinken und ist für den Einsatz von Kaktusdornen und Zweigen bei der Nahrungsaufnahme bekannt. Obwohl Spechtfinken genetisch dazu prädestiniert sind, während ihrer Ontogenese funktionellen Werkzeuggebrauch zu entwickeln, haben Laborstudien gezeigt, dass der Werkzeuggebrauch bei adulten Tieren dennoch plastisch und situationsbedingt selektiv ist. Dies, sowie der große Überlebenswert des Werkzeuggebrauchs, führt zu der Vermutung, dass der Werkzeuggebrauch und kognitive Fähigkeiten bei Spechtfinken in Koevolution entstanden sind, um die Entwicklung oder den Einsatz von Werkzeuggebrauch zu verbessern.

Ich untersuchte vor allen Dingen, ob Werkzeuggebrauch bei Spechtfinken in Verbindung mit erhöhten kognitiven Fähigkeiten entstanden ist, und wenn ja, ob diese auf den Bereich des Werkzeuggebrauchs beschränkt oder Teil einer allgemeineren kognitive Anpassung sind. Darüber hinaus habe ich die möglichen Voraussetzungen für die Evolution dieses ungewöhnlichen Verhaltens untersucht.

Kapitel 1 vergleicht die Leistungen von Spechtfinken mit denen von Zweig-Darwinfinken (*Camarhynchus parvulus*), einer nahe verwandten Art, die keine Werkzeuge benutzt. Diese vergleichende Studie umfasste sowohl allgemeinen Lernaufgaben (reversibles Lernen und Lösen neuartiger Probleme) als auch zwei Tests im Bereich der physikalischen Kognition, die Werkzeuggebrauch beinhalteten. "Physikalische Kognition" bezieht sich dabei auf die Fähigkeit, aus physikalischen Kräften der Umwelt allgemeingültige Regeln zu entwickeln. In Kapitel 2 erweiterte ich diesen Vergleich um einen weiteren Aspekt der physikalischen Kognition (dem Erkennen allgemeiner physikalischer Wechselbeziehungen) — unter Verwendung eines weit verbreiteten Versuchsmodells, der so genannten "Röhrenfallenaufgabe" (trap tube). Die Ergebnisse lieferten keine Hinweise auf höhere kognitive Fähigkeiten bei Spechtfinken im physikalischen Bereich (Kapitel 1-2). Tatsächlich lässt die hohe Flexibilität der Zweig-Darwinfinken beim reversiblen Lernen und deren hohe Leistung in den Versuchen zur physikalischen Kognition vermuten, dass die kognitiven Fähigkeiten, die für den Werkzeuggebrauch notwendig sind, bereits vor dem Werkzeuggebrauch selbst evoluiert wurden. Diese Hypothese wird in Kapitel 4 vertiefend aufgegriffen. Obwohl die werkzeuggebrauchenden Spechtfinken im Test zum reversiblen Lernen weniger flexibel waren, zeigten sie größeren Erfolg beim Erlernen einer neuartigen operanten Aufgabe.

Kapitel 3 untersucht mit zwei modifizierten Versuchsansätzen die Hypothese, dass das Defizit der Spechtfinken beim reversiblen Lernen (Kapitel 1) mit deren Form des Nahrungserwerbs einhergeht: Abgesehen vom Stochern mit Hilfe von Werkzeug hacken Spechtfinken oft lange auf das Substrat ein, um verdeckte Beute zu erreichen. Diese Beharrlichkeit ist sicherlich sinnvoll beim Nahrungserwerb, könnte aber auch zu einer geringeren Empfänglichkeit für Veränderungen des Belohnungsschemas im Versuchsaufbau führen. Deshalb verglich ich die Reaktionen von Specht- und Zweig-Darwinfinken in einem neuen Aufbau zu reversiblen Lernen, um die Ursachen der in Kapitel 2 gefundenen Unterschiede in der Flexibilität zu ermitteln. Zusätzlich untersuchte ich eventuelle Artunterschiede in Reaktionen auf neuartige Situationen. Die Arten unterschieden sich im Grad der Neophobie, jedoch nicht der Neophilie; Spechtfinken verhielten sich weniger ängstlich gegenüber neuen Objekten als Zweig-Darwinfinken. Ich fand keine Bestätigung dafür, dass die geringe Flexibilität der Spechtfinken an deren Unfähigkeit lag, eine zuvor gelernte positive Assoziation zu unterdrücken. Interessanterweise deuten einige Befunde in Kapitel 3 an, dass Individuen, die langsam im Untersuchen neuer Situationen sind, schneller im reversiblen Lernen sein könnten. Allerdings konnten weitere Untersuchungen diesen Zusammenhang nicht bestätigen.

Im letzten Kapitel (Kapitel 4) werden kognitive Fähigkeiten als mögliche Präadaptation für Werkzeuggebrauch diskutiert. Werkzeuggebrauch bei Darwinfinken könnte eine Erscheinungsform von kognitiven Fähigkeiten sein, die möglicherweise bereits vor dessen Entstehung vorhanden waren und die Evolution von Werkzeuggebrauch bei Spechtfinken erleichterten. Im Besonderen suchte ich nach Belegen für die Hypothese, dass eine Stammart mit sehr flexiblem Verhalten die schnelle und ausgedehnte Radiation der Darwinfinken erklären könnte. Am stärksten unterstützt wurde diese Hypothese durch die hohe Flexibilität der Darwinfinken, selbst im Vergleich zu anderen innovativen Arten, sowie durch die hohe Anzahl ungewöhnlicher Anpassungen im Bereich des Nahrungserwerbs. Allerdings stehen andere Resultate, wie das Fehlen von Unterschieden im Explorationsverhalten zwischen Darwinfinken und anderen Singvögeln, die auf Galápagos keine Radiation erfahren haben, nicht im Einklang mit dieser Hypothese.

Die Ergebnisse meiner Dissertation — in Verbindung mit den bereits vorhandenen Erkenntnissen über den adaptiven Wert von Werkzeuggebrauch bei Spechtfinken, dessen ontogenetische Entwicklung und den assoziierten kognitiven Fähigkeiten — bringen uns einem vollständigeren Verständnis des Werkzeuggebrauchs näher. Dabei wurde deutlich, wie wichtig es ist, nicht nur proximate Aspekte des Werkzeuggebrauchs bei Tieren zu untersuchen, sondern auch, dieses bemerkenswerte Verhalten im evolutionären Kontext zu betrachten.

## ACKNOWLEDGEMENTS

---

There are many people who contributed, in one way or another, greatly to the completion of my thesis. I would like to begin by thanking Sabine Tebbich for her support and supervision in all facets of my thesis from the outset. Sabine has been an inspiring mentor and instrumental in my personal growth as a scientist. She has also been a patient and encouraging role model who welcomed me with open arms from the get-go. On the subject of welcoming me with open arms: I am also very thankful for the hospitality that her husband Patrick and son Luca have shown me not only in the field but also on several of my work visits to their home, first in St Andrews, Scotland and later in their home in Vienna, where I ensconced myself in Luca's playroom. Apart from his hospitality, without which my cooperation with Sabine would never have been possible, Patrick has also made a number of invaluable contributions to this project in the form of field work, testing of animals in the lab and in particular the organisation of data processing in the field.

I dread the thought of not having had the encouragement and help of Henrik Brumm during these eventful thesis years: the better passages of this thesis were conceived in the aftermath of his exceptional homemade Spätzle. Henrik has always provided stability and excellent advice and showed much patience and understanding during my long months abroad in the Galápagos and elsewhere. In the final stages of writing, Henrik greatly helped me by proof-reading large parts of my thesis and making constructive suggestions pertaining to its structure and layout. Roger Mundry kindly provided extensive statistical instruction which helped me to conduct the analysis of chapter 1...thanks!! I also thank Sue Anne Zollinger for making drawings to make my thesis look pretty and also Nana Hesler who helped me with my German thesis summary.

Bart Kempenaers also provided support in many ways and I spent three pleasant years in his Behavioural Ecology and Evolutionary Genetics Research Group. During this time, I not only benefited from the companionship and advice of the many competent and friendly colleagues and friends there, but I also enjoyed the expertise of Wolfgang Forstmeier who

never hesitated to give me advise when needed.

Alex Kacelnik and Alex Weir have been a scientific and personal inspiration since I met them while doing my master's thesis at the University of Oxford. I feel very lucky indeed to have had the opportunity to collaborate with them again in the context of this project.

Field work on the Galápagos was an involved, joint-venture that only culminated in a successful outcome due to the efforts of many people—efforts which often went far beyond the call of duty. Unfortunately, I will have to restrict myself to a few people to avoid turning this into the longest chapter of my thesis!

Birgit Fessl and Sharon Deem were both unusually kind, congenial colleagues and friends, who were the source of invaluable knowledge in the Galápagos. I am also exceedingly grateful to my field assistant Sophia Stankewitz who was resourceful and helped me to overcome the many doubts and challenges that accompany field work and the “growing pains” that go hand in hand with completing a doctoral thesis. The many local field assistants, in particular Viviana Morales, Mari Cruz Jaramillo, Tania Quisingo Chiza, Paola Buitron Lopez, and Eduardo Sandoval not only helped me with my field work but also aided me in navigating a new culture and ensured that I didn't starve when waiters could not decipher my rudimentary spanish (well, at least I tried). Caroline Raby and Erica Cartmill, two non-local and particularly dedicated scientists journeyed from Chicago and Britain respectively in order to share their competence and uncommon humour with me. Martin Wikelski generously provided radio-telemetry equipment that allowed us to assess the condition of the finches upon their release after being held some time in captivity. Unfortunatley I was not able to finish the write-up of this data in time for the submission of my thesis, but it is up-and-coming.

Finally, I turn to the hard core of friends and family who have always been encouraging and supportive in countless ways. I feel very lucky to have these people by my side. My close friends, are strewn throughtout the world and thus I don't get to see them nearly as often as I'd like. Nevertheless, they have been very helpful and seem to be with me in spirit if not actually “by my side”. I would like to specifically thank Tine and Nana (Copenhagen), Karen, Marie, and Shirin (Berlin), Lindsay (Washington DC) and Britta (Phnom Penh) for their friendship without which my world would be an indescribably duller place. Of course, I am especially grateful to my parents and sister for the unconditional and loving support that they have given me through the years. In particular my father has been an intellectual inspiration and has helped me to build up the confidence for this venture. I would also like to thank the Scenna family who have supported me always. Ginny, you are last but not least in my thoughts--I thank you from the bottom of my for being such a good friend and role vmodel. I miss you!

## REFERENCES

---

- Abs, M., Curio, E., Kramer, P. & Niethammer, J.** 1965. Zur Ernährungsweise der Eulen auf Galapagos Ergebnisse der Deutschen Galapagos Expedition 1962/ 63. IX. Journal of Ornithology, 106, 49-57.
- Alcock, J.** 1972. The evolution of the use of tools by feeding animals. *Evolution*, 26, 464-473.
- Ancel, L. W.** 1999. A Quantitative Model of the Simpson-Baldwin Effect. *Journal of Theoretical Biology*, 196, 197-209.
- Arbogast, B. S., Drovetski, S. V., Curry, R. L., Boag, P. T., Seutin, G., Grant, P. R., Grant, B. R. & Anderson, D. J.** 2006. The origin and diversification of Galapagos Mockingbirds. *Evolution*, 60, 370-382.
- Auersperg, A.** submitted. Flexibility in problem solving and tool use of Keas and New Caledonian crows in a Multi Access Box paradigm.
- Auersperg, A. M. I., Gajdon, G. K. & Huber, L.** 2009. Kea (*Nestor notabilis*) consider spatial relationships between objects in the support problem. *Biology Letters*, 5, 455-458.
- Avital, E. & Jablonka, E.** 2000. Animal traditions: behavioural inheritance in evolution. Cambridge: Cambridge University Press.
- Baayen, R.** 2008. Analyzing Linguistic Data, 1 edn. Cambridge: Cambridge University Press.
- Balda, R. P. & Kamil, A. C.** 1989. A comparative study of cache recovery by three corvid species. *Animal Behaviour*, 38, 486-495.
- Bates, D. & Maechler, M.** 2009. lme4: Linear mixed-effects models using S4 classes.
- Bateson, P.** 2004. The Active Role of Behaviour in Evolution. *Biology and Philosophy*, 19, 283-298.
- Beck, B. B.** 1980. Animal tool behavior: the use and manufacture of tools by animals. New York, NY: Garland.
- Beck, B. B.** 1986. Tools and intelligence. In: *Animal intelligence: Insights into the animal mind* (Ed. by Hoage, R. J. & Goldman, L.), pp. 135-147. Washington D.C.: Smithsonian Institution Press.
- Bentley-Condit, V. K. & Smith, E. O.** 2009. Animal tool use: current definitions and an updated comprehensive catalog. *Behaviour*, 147, 185-221.
- Bird, C. D. & Emery, N. J.** 2009. Insightful problem solving and creative tool modification by captive non-tool-using rooks. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 10370-10375.
- Biro, D., Inoue-Nakamura, N., Tonooka, R., Yamakoshi, G., Sousa, C. & Matsuzawa, T.** 2003. Cultural innovation and transmission of tool use in wild chimpanzees: evidence from field experiments. *Animal Cognition*, 6, 213 - 223.

- Bitterman, M. E.** 1960. Toward a comparative psychology of learning. *American Psychologist*, 15, 704-712.
- Bittermann, M. E.** 1965. Phyletic differences in learning. *American Psychologist*, 20, 396-410.
- Bluff, L. A., Weir, A. A. S., Rutz, C., Wimpenny, J. H. & Kacelnik, A.** 2007. Tool-related cognition in New Caledonian crows. *Comparative Cognition & Behavior Reviews*, 2, 1-2.
- Bolhuis, J. J. & MacPhail, E. M.** 2001. A critique of the neuroecology of learning and memory. *Trends in Cognitive Sciences*, 5, 426-433.
- Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J.-S. S.** 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, 24, 127-135.
- Bollmer, J. L., Kimball, R. T., Whiteman, N. K., Sarasola, J. H. & Parker, P. G.** 2006. Phylogeography of the Galápagos hawk (*Buteo galapagoensis*): A recent arrival to the Galápagos Islands. *Molecular Phylogenetics and Evolution*, 39, 237-247.
- Bond, A. B., Kamil, A. C. & Balda, R. P.** 2007. Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus*, *Nucifraga columbiana*, *Aphelocoma californica*). *Journal of Comparative Psychology*, 121, 372-379.
- Boogert, N. J., Reader, S. M. & Laland, K. N.** 2006. The relation between social rank, neophobia and individual learning in starlings. *Animal Behaviour*, 72, 1229-1239.
- Bowman, R. I. & Billeb, S. L.** 1965. Blood-eating in a Galápagos finch. *The Living Bird*, 4, 29-44.
- Breuer, T., Ndoundou-Hockemba, M. & Fishlock, V.** 2005. First Observation of Tool Use in Wild Gorillas. *PLoS Biology*, 3, e380.
- Browne, R. A., Collins, E. & Anderson, D. J.** 2008. Genetic structure of Galapagos populations of the yellow warbler. *Condor*, 110, 549-553.
- Burns, K. J., Hackett, S. J. & Klein, N. K.** 2002. Phylogenetic relationships and morphological diversity in Darwin's finches and their relatives. *Evolution*, 1240-1252.
- Byrne, R. W.** 1995. *The thinking ape: Evolutionary origins of intelligence*. Oxford, UK: Oxford University Press.
- Byrne, R. W. & Bates, L. A.** 2006. Why are animals cognitive? *Current Biology*, 16, R445-R448.
- Chaffer, N.** 1945. The spotted and satin bower-birds: A comparison. *Emu*, XLIV, 161-181.
- Chance, M. R. A. & Meade, A. P.** 1955. Competition between feeding and exploration in the rat. *Behaviour*, 8, 174-182.
- Chappell, J.** 2006. Avian Cognition: Understanding Tool Use. *Current Biology*, 16, R244-R245.
- Chappell, J. & Kacelnik, A.** 2002. Tool selectivity in a non-mammal, the New Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, 5, 71-78.
- Chappell, J. & Kacelnik, A.** 2004. Selection of tool diameter by New Caledonian crows *Corvus moneduloides*. *Animal Cognition*, 7, 121-127.
- Chevalier-Skolnikoff, S. & Liska, J. O.** 1993. Tool use by wild and captive elephants. *Animal Behaviour*, 46, 209-219.
- Conover, W. J., Johnson, M.E., and Johnson M. M.** 1981. A comparative study of tests for homogeneity of variances, with applications to the outer continental shelf bidding data. *Technometrics*, 23, 351-361.
- Curio, E. & Kramer, P.** 1964. Vom mangrove-finken (*Cactospiza heliobates* Snodgrass und Heller). *Zeitschrift für Tierpsychologie*, 21, 223-234.
- Curry, R. L. & Anderson, D. J.** 1987. Interisland variation in blood drinking by Galápagos mockingbirds. *Auk*, 104, 517-521.
- Davey, G.** 1989. *Ecological learning theory*. London: Routledge.
- Dawkins, R.** 1996. *Climbing mount improbable*. New York, NY: W.W. Norton.

- Day, L. B., Crews, D. & Wilczynski, W.** 1999. Spatial and reversal learning in congeneric lizards with different foraging strategies. *Animal Behaviour*, 57, 393-407.
- Day, R. L., Coe, R. L., Kendal, J. R. & Laland, K. N.** 2003. Neophilia, innovation and social learning: a study of intergeneric differences in callitrichid monkeys. *Animal Behaviour*, 65, 559-571.
- De Groot, R. S.** 1982. Origin, status and ecology of the owls in Galapagos. *Ardea*, 71, 167-182.
- DeBenedictis, P. A.** 1966. The bill-brace feeding behaviour of the Galápagos finch *Geospiza conirostris*. *Condor*, 68, 206-&.
- Dingemans, N. J., Both, C., Drent, P. J., van Oers, K. & van Noordwijk, A. J.** 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, 64, 929-938.
- Drent, P. J. & Marchetti, C.** 1999. Individuality, exploration and foraging in hand raised juvenile great tits. In: Proceedings of the 22nd International Ornithological Congress (Ed. by Adams, N. J. & Slotow, R. H.), pp. 896-914. Durban, South Africa: BirdLife South Africa, Johannesburg.
- Eibl-Eibesfeldt, I.** 1961. Über den Werkzeuggebrauch des Spechtfinken *Camarhynchus pallidus* (Scalder und Salvin). *Zeitschrift für Tierpsychologie*, 18, 343-346.
- Eibl-Eibesfeldt, I. & Sielmann, H.** 1962. Beobachtungen am Spechtfinken *Cactospiza pallida* (Scalder und Salvin). *Journal of Ornithology*, 103, 92-101.
- Emery, N. J. & Clayton, N. S.** 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, 306, 1903-1907.
- Emery, N. J. & Clayton, N. S.** 2009. Tool use and physical cognition in birds and mammals. *Current Opinion in Neurobiology*, 19, 27-33.
- Fessl, B., Loaiza, A., Tebbich, S. & Young, H.** 2010. Feeding and nesting requirements of the critically endangered Mangrove Finch *Camarhynchus heliobates*. *Journal of Ornithology*, 1-8.
- Fung, K. P. & Lee, J.** 1989. Extensions of Fisher exact test to 2-by-K Contingency tables—a computer program in BASIC. *Biomedicine* 28:195-196. *Biomedicine*, 28, 196-196.
- Garcia, J., Ervin, F. R. & Koelling, R. A.** 1966. Learning with prolonged delay of reinforcement. *Psychonomic Science*, 5, 121-122.
- Garcia, J., Hankins, W. G. & Rusiniak, K. W.** 1974. Behavioral regulation of the milieu interne in man and rat. *Science*, 185, 824-831.
- Gauntlett-Gilbert, J., Roberts, R. C. & Brown, V. J.** 1999. Mechanisms underlying attentional set-shifting in Parkinsons disease. *Neuropsychologia*, 37, 605-616.
- Godfrey-Smith, P.** 2001. Environmental Complexity and the Evolution of Cognition. In: *The Evolution of Intelligence* (Ed. by Sternberg, R. J. & Kaufman, J. C.): Lawrence Erlbaum Associates.
- Goodall, J.** 1964. Tool-using and aimed throwing in a community of free-living chimpanzees. *Nature*, 201, 1264-1266.
- Grant, P. R.** 1986. *Ecology and evolution of Darwin's finches*. Princeton: Princeton University Press.
- Grant, P. R. & Boag, P. T.** 1980. Rainfall on the Galápagos and the demography of Darwin's finches. *Auk*, 97, 227-244.
- Grant, P. R. & Grant, B. R.** 1980. Annual variation in finch numbers, foraging and food supply on Isla Daphne Major, Galápagos. *Oecologia*, 46, 55-62.
- Grant, P. R. & Grant, B. R.** 2008. *How and why species multiply*. Princeton: Princeton University Press.
- Greenberg, R.** 1984. Differences in feeding neophobia in the tropical migrant woodwarblers *Dendroica castanea* and *D. pensylvanica*. *Journal of Comparative Psychology*, 98, 131-136.
- Greenberg, R. & Mettke-Hofmann, C.** 2001. Ecological Aspects of Neophobia and Neophilia in Birds. In: *Current Ornithology* (Ed. by Nolan, V. J. & Thompson, C.), pp. 119-178. New York: Kluwer Academic/Plenum Publishers.

- Gruber, T., Clay, Z. & Zuberbuhler, K.** 2010. A comparison of bonobo and chimpanzee tool use: evidence for a female bias in the Pan lineage. *Animal Behaviour*, 80, 1023-1033.
- Hall, K. R. L.** 1963. Tool-using performances as indicators of behavioural adaptability. *Current Anthropology*, 4, 479-494.
- Hamann, O.** 1981. Plant communities of the Galápagos Islands. *Dansk Botanisk Archiv*, 34, 1-63.
- Hansell, M. & Ruxton, G. D.** 2008. Setting tool use within the context of animal construction behaviour. *Trends in Ecology & Evolution*, 23, 73-78.
- Hansell, M. H.** 1987. What's so special about using tools? *New Scientist*, 8 January, 55-56.
- Hart, B. L. & Hart, L. A.** 1994. Fly switching by Asian elephants: tool use to control parasites. *Animal Behaviour*, 48, 35-45.
- Harvey, P. H. & Pagel, M. D.** 1991. *The comparative method in evolutionary biology*. Oxford: Oxford University Press.
- Hauser, M. D.** 1997. Artifactual kinds and functional design features: what a primate understands without language. *Cognition*, 64, 285-308.
- Hauser, M. D., Kralik, J. & Botto-Mahan, C.** 1999. Problem solving and functional design features: experiments on cotton-top tamarins, *Saguinus oedipus oedipus*. *Animal Behaviour*, 57, 565-582.
- Hauser, M. D., Pearson, H. & Seelig, D.** 2002a. Ontogeny of tool use in cottontop tamarins, *Saguinus oedipus*: innate recognition of functionally relevant features. *Animal Behaviour*, 64, 299-311.
- Hauser, M. D., Santos, L. R., Spaepen, G. M. & Pearson, H. E.** 2002b. Problem solving, inhibition and domain-specific experience: experiments on cottontop tamarins, *Saguinus oedipus*. *Animal Behaviour*, 64, 387-396.
- Healy, S. D., Bacon, I. E., Haggis, O., Harris, A. P. & Kelley, L. A.** 2009. Explanations for variation in cognitive ability: Behavioural ecology meets comparative cognition. *Behavioural Processes*, 80, 288-294.
- Healy, S. D., de Kort, S. R. & Clayton, N. S.** 2005. The hippocampus, spatial memory and food hoarding: a puzzle revisited. *Trends in Ecology & Evolution*, 20, 17-22.
- Herrmann, E., Wobber, V. & Call, J.** 2008. Great apes' (*Pan troglodytes*, *Pan paniscus*, *Gorilla gorilla*, *Pongo pygmaeus*) understanding of tool functional properties after limited experience. *Journal of Comparative Psychology*, 122, 220-230.
- Heyes, C. M.** 1993. Anecdotes, training, trapping and triangulating: Do animals attribute mental states? *Animal Behaviour*, 46, 177-188.
- Hinton, G. & Nowlan, S.** 1987. How learning can guide evolution. *Complex Systems*, 1, 495-502.
- Hogan, J. A.** 1965. An experimental study of conflict and fear: An analysis of behavior of young chicks towards a mealworm. Part I. The behavior of chicks which do not eat the mealworm. *Behaviour*, 25, 45-97.
- Hughes, R. N.** 1997. Intrinsic exploration in animals: motives and measurements. *Behavioural Processes*, 41, 213-226.
- Hundley, M.** 1963. Notes on methods of feeding and the use of tools in the Geospizinae. *Auk*, 80, 372-373.
- Hunt, G. R.** 1996. Manufacture and use of hook-tools by New Caledonian crows. *Nature*, 379, 249-251.
- Hunt, G. R. & Gray, R. D.** 2002. Species-wide manufacture of stick-type tools by New Caledonian Crows. *Emu*, 102, 349-353.
- Hunt, G. R. & Gray, R. D.** 2004a. The crafting of hook tools by wild New Caledonian crows. *Proceedings of the Royal Society of London B*, 271, S88-S90.
- Hunt, G. R. & Gray, R. D.** 2004b. Direct observations of pandanus-tool manufacture and use by a New Caledonian crow (*Corvus moneduloides*). *Animal Cognition*, 7, 114-120.
- Inoue-Nakamura, N. & Matsuzawa, T.** 1997. Development of stone tool use by wild chimpanzees (*Pan*

- trogodytes*). *Journal of Comparative Psychology*, 111, 159-173.
- Iwaniuk, A. N., Wylie, D., R. & Lefebvre, L.** 2009. The comparative approach and brain-behaviour relationships: a tool for understanding tool use. *Canadian Journal of Experimental Psychology*, 63, 150-159.
- Jablunka, E. & Lamb, M.** 2005. *Evolution in four dimensions*. Cambridge, MA: MIT Press.
- Jackson, M. H.** 1993. *Galápagos: A Natural History*. Calgary: University of Calgary Press.
- Jones, C. B.** 2005. *Behavioral flexibility in primates: Causes and consequences*. New York: Springer Verlag.
- Kacelnik, A.** 2009. Tools for thought or thoughts for tools? *Proceedings of the Academy of Natural Sciences of the United States of America*, 106, 10071-10072.
- Kacelnik, A., Chappell, J., Weir, A. A. S. & Kenward, B.** 2006. Cognitive adaptations for tool-related behaviour in New Caledonian Crows. In: *Comparative cognition: experimental explorations of animal intelligence* (Ed. by Wasserman, E. A. & Zentall, T. R.), pp. 515-528. Oxford: Oxford University Press.
- Kenward, B., Rutz, C., Weir, A. A. S. & Kacelnik, A.** 2006. Development of tool use in New Caledonian crows: inherited action patterns and social influences. *Animal Behaviour*, 72, 1329-1343.
- Kenward, B., Weir, A. A. S., Rutz, C. & Kacelnik, A.** 2005. Tool manufacture by naive juvenile crows. *Nature*, 433, 121.
- Krützen, M., Mann, J., Heithaus, M. R., Connor, R. C., Bejder, L. & Sherwin, W. B.** 2005. Cultural transmission of tool use in bottlenose dolphins. *Proceedings of the National Academy of Sciences of the United States of America*, 102, 8939-8943.
- Kummer, H. & Goodall, J.** 1985. Conditions of innovative behaviour in primates. *Philosophical Transactions of the Royal Society of London B*, 308, 203-214.
- Lack, D.** 1947. *Darwin's finches*. Cambridge: Cambridge University Press.
- Laland, K. N.** 2008. Exploring gene-culture interactions: insights from handedness, sexual selection and niche-construction case studies. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 3577-3589.
- Laverty, T. M. & Plowright, R. C.** 1988. Flower handling by bumblebees: a comparison of specialists and generalists. *Animal Behaviour*, 36, 733-740.
- Lefebvre, L., Nicolakakis, N. & Boire, D.** 2002. Tools and brains in birds. *Behaviour*, 139, 939-973.
- Lewontin, R. C.** 1978. *Adaptation*. *Scientific American*, 239, 156-169.
- Lewontin, R. C.** 1982. Organism and environment. In: *Learning, development and culture* (Ed. by Plotkin, H. C.), pp. 151-170. New York, NY: Wiley.
- Liedtke, J., Werdnich, D., Gajdon, G., Huber, L. & Wanker, R.** 2010. Big brains are not enough: performance of three parrot species in the trap-tube paradigm. *Animal Cognition*, 1-7.
- Limongelli, L., Boysen, S. T. & Visalberghi, E.** 1995. Comprehension of cause-effect relations in a tool-using task by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, 109, 18-26.
- Lissek, B., Diekamp, B. & Güntürkün, O.** 2002. Impaired Learning of a Color Reversal Task After NMDA Receptor Blockade in the Pigeon (*Columba livia*) Associative Forebrain (Neostriatum Caudolaterale). *Behavioral Neuroscience*, 116, 523-529.
- Lonsdorf, E.** 2006. What is the role of mothers in the acquisition of termite-fishing behaviors in wild chimpanzees (*Pan troglodytes schweinfurthii*)? *Animal Cognition*, 9, 36-46.
- Lonsdorf, E. V., Ross, S. R., Linick, S. A., Milstein, M. S. & Melber, T. N.** 2009. An experimental, comparative investigation of tool use in chimpanzees and gorillas. *Animal Behaviour*, 77, 1119-1126.
- MacFarland, C. & Reeder, W.** 1974. Cleaning symbiosis involving Galápagos tortoise and two species of Darwin's finches. *Zeitschrift fuer Tierpsychologie*, 34.
- Mackintosh, N. J. & Holgate, V.** 1969. Serial reversal training and nonreversal shift learning. *Journal of Comparative and Physiological Psychology*, 67, 89-93.

- Mackintosh, N. J., McGonigle, B., Holgate, V. & Vanderver, V.** 1968. Factors underlying improvement in serial reversal learning. *Canadian Journal of Psychology*, 22, 85-95.
- Mann, J., Sargeant, B. L., Watson-Capps, J. J., Gibson, Q. A., Heithaus, M. R., Connor, R. C. & Patterson, E.** 2008. Why Do Dolphins Carry Sponges? *PLoS ONE*, 3, e3868.
- Manrique, H. M., Gross, A. N.-M. & Call, J.** 2010. Great apes select tools on the basis of their rigidity. *Journal of Experimental Psychology: Animal Behavior Processes*, online first.
- Marchetti, C. & Drent, P. J.** 2000. Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour*, 60, 131-140.
- Martin-Ordas, G., Call, J. & Colmenares, F.** 2008. Tubes, tables and traps: great apes solve two functionally equivalent trap tasks but show no evidence of transfer across tasks. *Animal Cognition*, 11, 423-430.
- McGrew, W. C.** 2010. Chimpanzee Technology. *Science*, 328, 579-580.
- Mehlhorn, J., Hunt, G. R., Gray, R. D., Rehkämper, G. & Güntürkün, O.** 2010. Tool-Making New Caledonian Crows Have Large Associative Brain Areas. *Brain, Behavior and Evolution*, 75, 63-70.
- Mettke-Hofmann, C., Winkler, H. & Leisler, B.** 2002. The Significance of Ecological Factors for Exploration and Neophobia in Parrots. *Ethology*, 108, 249-272.
- Millikan, G. & Bowman, R.** 1967. Observations on Galapagos tool-using finches in captivity. *Living Bird*, 6, 23-41.
- Montgomery, K. C.** 1955. The relation between fear induced by novel stimulation and exploratory behavior. *Comp. Phys. Psych.*, 48, 254-260.
- Morse, D. H.** 1980. *Behavioural mechanisms of ecology*. Cambridge, MA: Harvard University Press.
- Mulcahy, N. & Call, J.** 2006. How great apes perform on a modified trap-tube task. *Animal Cognition*, 9, 193-199.
- Nicolakakis, N., Sol, D. & Lefebvre, L.** 2003. Behavioural flexibility predicts species richness in birds, but not extinction risk. *Animal Behaviour*, 65, 445-452.
- Oakley, K. P.** 1949. *Man the tool-maker*. London: British Museum.
- Odling-Smee, F. J., Laland, K. N. & Feldman, M. W.** 2003. *Niche construction: the neglected process in evolution*. Princeton, NJ: Princeton University Press.
- Ottoni, E. B. & Izar, P.** 2008. Capuchin monkey tool use: Overview and implications. *Evolutionary Anthropology*, 17, 171-178.
- Overington, S. E., Morand-Ferron, J., Boogert, N. J. & Lefebvre, L.** 2009. Technical innovations drive the relationship between innovativeness and residual brain size in birds. *Animal Behaviour*, 78, 1001-1010.
- Parent, C. E., Caccone, A. & Petren, K.** 2008. Colonization and diversification of Galápagos terrestrial fauna: a phylogenetic and biogeographical synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 363, 3347-3361.
- Parker, S. T. & Gibson, K. R.** 1977. Object manipulation, tool use and sensorimotor intelligence as feeding adaptations in Cebus monkeys and great apes. *Journal of Human Evolution*, 6, 623-641.
- Parker, S. T. & Gibson, K. R.** 1979. A developmental model for the evolution of language and intelligence in early hominids. *Behavioral and Brain Sciences*, 2, 367-407.
- Peckham, G. W. & Peckham, E. G.** 1898. On the instincts and habits of the solitary wasps. *Wisconsin Geological and Natural History Survey*, 2, 1-245.
- Penn, D. C., Holyoak, K. J. & Povinelli, D. J.** 2008. Darwin's mistake: Explaining the discontinuity between human and nonhuman minds. *Behavioral and Brain Sciences*, 31, 109-178.
- Penn, D. C. & Povinelli, D. J.** 2007. Causal Cognition in Human and Nonhuman Animals: A Comparative, Critical Review. *Annual Review of Psychology*, 58, 97-118.
- Petren, K., Grant, B. R. & Grant, P. R.** 1999. A phylogeny of Darwin's finches based on microsatellite DNA

- length variation. *Proceedings of the Royal Society B: Biological Sciences*, 266, 321.
- Petren, K., Grant, B. R., Grant, P. R. & Keller, L. F.** 2005. Comparative landscape genetics and the adaptive radiation of Darwin's finches: the role of peripheral isolation. *Molecular Ecology*, 14, 2943-2957.
- Pouydebat, E., Berge, C., Gorce, P. & Coppens, Y.** 2005. Use and manufacture of tools to extract food by captive *Gorilla gorilla gorilla*: Experimental approach. *Folia Primatologica*, 76, 180-183.
- Povinelli, D. J.** 2000. *Folk Physics for Apes*. Oxford, UK: Oxford University Press.
- Price, T.** 2008. *Speciation in birds*. Greenwood Village: Roberts & Company Publishers.
- Raach, A. & Leisler, B.** 1989. Auswirkungen der Jugenderfahrung auf die Wahl von Habitatstrukturen und auf das Erkundungsverhalten des Mariskensängers (*Acrocephalus melanopogon*). *Journal für Ornithologie*, 130, 256-259.
- Ratcliffe, J. M., Fenton, M. B. & Galef, B. G.** 2003. An exception to the rule: common vampire bats do not learn taste aversions. *Animal Behaviour*, 65, 385-389.
- Reader, S. M. & Laland, K. N.** 2002. Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences, USA*, 99, 4436-4441.
- Reader, S. M. & Laland, K. N.** 2003. *Animal innovation*. Oxford: Oxford University Press.
- Rehkämper, G., Frahm, H. D. & Zilles, K.** 1991. Quantitative development of brain and brain structures in birds (Galliformes and Passeriformes) compared to that in mammals (Insectivores and Primates). *Brain, Behavior and Evolution*, 37, 125-143.
- Robinson, M. H.** 1990. Predator-prey interactions, informational complexity, and the origins of intelligence. In: *Insect defenses: Adaptive mechanisms and strategies of prey and predators* (Ed. by Schmidt, D. L. E. J. O.), pp. 129-149. Albany: State University of New York Press.
- Ross, D. M.** 1971. Protection of hermit crabs (*Dardanus spp.*) from octopus by commensal sea anemones (*Calliactis spp.*). *Nature*, 230, 401-402.
- Roth, T. C., LaDage, L. D. & Pravosudov, V. V.** 2010. Learning capabilities enhanced in harsh environments: a common garden approach. *Proceedings of the Royal Society B: Biological Sciences*, 277, 3187-3193.
- Rozin, P. & Kalat, J. W.** 1971. Specific hungers and poison avoidance as adaptive specializations of learning. *Psychological Review*, 78, 459-486.
- Russell, P. A.** 1973. Relationship between exploratory behaviour and fear: a review. *British Journal of Psychology*, 64, 417-433.
- Santos, L. R., Mahajan, N. & Barnes, J.** 2005a. How prosimian primates represent tools: Experiments with two lemur species (*Eulemur fulvus* and *Lemur catta*). *Journal of Comparative Psychology*, 119, 394-403.
- Santos, L. R., Pearson, H. M., Spaepen, G. M., Tsao, F. & Hauser, M. D.** 2006a. Probing the limits of tool competence: Experiments with two non-tool-using species (*Cercopithecus aethiops* and *Saguinus oedipus*). *Animal Cognition*, 9, 94-109.
- Santos, L. R., Rosati, A., Sproul, C., Spaulding, B. & Hauser, M. D.** 2005b. Means-means-end tool choice in cotton-top tamarins (*Saguinus oedipus*): finding the limits on primates' knowledge of tools. *Animal Cognition*, online first.
- Santos, L. R., Seelig, D. & Hauser, M. D.** 2006b. Cotton-top Tamarins' (*Saguinus oedipus*) expectations about occluded objects: A dissociation between looking and reaching tasks. *Infancy*, 9, 147-171.
- Sato, A., Tichy, H., O'hUigin, C., Grant, P. R., Grant, B. R. & Klein, J.** 2001. On the Origin of Darwin's Finches. *Molecular Biology and Evolution*, 18, 299-311.
- Schielzeth, H. & Forstmeier, W.** 2009. Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology*, 20, 416-420.
- Schluter, D.** 1984. Feeding correlates of breeding and social organization in two Galápagos finches. *Auk*, 101, 59-68.

- Schluter, D.** 2000. The ecology of adaptive radiation. New York, NY: Oxford University Press.
- Schluter, D. & Grant, P. R.** 1984. Ecological correlates of morphological evolution in a Darwin's finch, *Geospiza difficilis*. *Evolution*, 38, 856-869.
- Seed, A. & Byrne, R.** 2010. Animal Tool-Use. *Current biology* : CB, 20, R1032-R1039.
- Seed, A., Emery, N. & Clayton, N.** 2009a. Intelligence in Corvids and Apes: A Case of Convergent Evolution? *Ethology*, 115, 401-420.
- Seed, A. M., Call, J., Emery, N. J. & Clayton, N. S.** 2009b. Chimpanzees solve the trap problem when the confound of tool-use is removed. *Journal of Experimental Psychology: Animal Behavior Processes*, 35, 23-34.
- Seed, A. M., Tebbich, S., Emery, N. J. & Clayton, N. S.** 2006. Investigating Physical Cognition in Rooks, *Corvus frugilegus*. *Current Biology*, 16, 697-701.
- Seferta, A., Guay, P. J., Marzinotto, E. & Lefebvre, L.** 2001. Learning differences between feral pigeons and zenaida doves: The role of neophobia and human proximity. *Ethology*, 107, 281-293.
- Shettleworth, S. J.** 1993. Where is the comparison in comparative cognition? Alternative research programs. *Psychological Science*, 4, 179-184.
- Shettleworth, S. J.** 1998. Cognition, evolution, and behavior. London: Oxford University Press.
- Shettleworth, S. J.** 2003. Memory and hippocampal specialization in food-storing birds: challenges for research on comparative cognition. *Brain, Behavior and Evolution*, 62, 108-116.
- Shettleworth, S. J.** 2010. Clever animals and killjoy explanations in comparative psychology. *Trends in Cognitive Sciences*, 14, 477-481.
- Silva, F. J., Page, D. M. & Silva, K. M.** 2005. Methodological-conceptual problems in the study of chimpanzees' folk physics: How studies with adult humans can help. *Learning & Behavior*, 33, 47-58.
- Smolker, R., Richards, A., Connor, R., Mann, J. & Berggren, P.** 1997. Sponge carrying by dolphins (*Delphinidae, Tursiops sp.*): A foraging specialization involving tool use? *Ethology*, 103, 454-465.
- Smulders, T. V., Gould, K. L. & Leaver, L. A.** 2010. Using ecology to guide the study of cognitive and neural mechanisms of different aspects of spatial memory in food-hoarding animals. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 883-900.
- Snedecor, G. W. & Cochran, W. G.** 1989. *Statistical Methods*, 8 edn: Iowa State University Press.
- Sol, D.** 2003. Behavioural flexibility: a neglected issue in the ecological and evolutionary literature? In: *Animal innovation* (Ed. by Reader, S. M. & Laland, K. N.), pp. 63-82. Oxford, UK: Oxford University Press.
- Sol, D., Stirling, D. G. & Lefebvre, L.** 2005. Behavioral drive or behavioral inhibition in evolution: subspecific diversification in Holarctic passerines. *Evolution*, 59, 2669-2677.
- Spaulding, B. & Hauser, M. D.** 2005. What experience is required for acquiring tool competence? Experiments with two Callitrichids. *Animal Behaviour*, 70, 517-526.
- St Amant, R. & Horton, T. E.** 2008. Revisiting the definition of animal tool use. *Animal Behaviour*, 75, 1199-1208.
- Stevens, J. R., Hallinan, E. V. & Hauser, M. D.** 2005. The ecology and evolution of patience in two New World monkeys. *Biology Letters*, 1, 223-226.
- Tait, D. S. & Brown, V. J.** 2007. Difficulty overcoming learned non-reward during reversal learning in rats with ibotenic acid lesions of orbital prefrontal cortex. *Annals of the New York Academy of Sciences*, 1121, 407-420.
- Taylor, A. H., Hunt, G. R., Holzhaider, J. C. & Gray, R. D.** 2007. Spontaneous Metatool Use by New Caledonian Crows. *Current Biology*, 17, 1504-1507.
- Taylor, A. H., Hunt, G. R., Medina, F. S. & Gray, R. D.** 2009a. Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society B: Biological Sciences*, 276, 247-254.

- Taylor, A. H., Roberts, R., Hunt, G. & Gray, R.** 2009b. Causal reasoning in New Caledonian crows: Ruling out spatial analogies and sampling error. *Communicative and Integrative Biology*, 2.
- Tebbich, S. & Bshary, R.** 2004. Cognitive abilities related to tool use in the woodpecker finch, *Cactospiza pallida*. *Animal Behaviour*, 67, 689-697.
- Tebbich, S., Fessl, B. & Blomqvist, D.** 2009a. Exploration and ecology in Darwin's finches. *Evolutionary Ecology*, 23, 591-605.
- Tebbich, S., Seed, A. M., Emery, N. J. & Clayton, N. S.** 2007. Non-tool-using rooks, *Corvus frugilegus*, solve the trap-tube problem. *Animal Cognition*, 10, 225-231.
- Tebbich, S., Sterelny, K. & Teschke, I.** 2010. The tale of the finch: adaptive radiation and behavioural flexibility. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 1099-1109.
- Tebbich, S., Taborsky, M., Fessl, B. & Blomqvist, D.** 2001. Do woodpecker finches acquire tool-use by social learning? *Proceedings of the Royal Society of London B*, 268, 2189-2193.
- Tebbich, S., Taborsky, M., Fessl, B. & Dvorak, M.** 2002. The ecology of tool-use in the woodpecker finch (*Cactospiza pallida*). *Ecology Letters*, 5, 656-664.
- Tebbich, S., Taborsky, M., Fessl, B., Dvorak, M. & Winkler, H.** 2004. Feeding behavior of four arboreal Darwin's finches: adaptations to spatial and seasonal variability. *Condor*, 106, 95-105.
- Thomsen, L. R., Campbell, R. D. & Rosell, F.** 2007. Tool-use in a display behaviour by Eurasian beavers (*Castor fiber*). *Animal Cognition*, 10, 477-482.
- Thorpe, W. H.** 1956. *Learning and instinct in animals*. London.: Methuen and Co. LTD.
- Tomasello, M. & Call, J.** 1997. *Primate cognition*. New York, NY: Oxford University Press.
- van Lawick-Goodall, J.** 1970. Tool-using in primates and other vertebrates. In: *Advances in the Study of Behavior* (Ed. by Lehrman, D., Hinde, R. & Shaw, E.), pp. 195-249. New York, NY: Academic Press.
- van Lawick-Goodall, J. & van Lawick, H.** 1966. Use of tools by the Egyptian vulture, *Neophron percnopterus*. *Nature*, 212, 1468-1469.
- van Schaik, C. P., Ancrenaz, M., Borgen, G., Galdikas, B., Knott, C. D., Singleton, I., Suzuki, A., Utami, S. S. & Merrill, M.** 2003. Orangutan cultures and the evolution of material culture. *Science*, 299, 102-105.
- Verbeek, M. E. M., Drent, P. J. & Wiepkema, P. R.** 1994. Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, 48, 1113-1121.
- Vincek, V., O'Huigin, C., Satta, Y., Takahata, N., Boag, P. T., Grant, P. R., Grant, B. R. & Klein, J.** 1997. How large was the founding population of Darwin's finches? *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 264, 111-118.
- Visalberghi, E. & Limongelli, L.** 1994. Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, 108, 15-22.
- Visalberghi, E. & Tomasello, M.** 1998. Primate causal understanding in the physical and psychological domains. *Behavioural Processes*, 42, 189-203.
- Vitale, A., Visalberghi, E. & De Lillo, C.** 1991. Responses to a snake model in captive crab-eating macaques (*Macaca fascicularis*) and captive tufted capuchins (*Cebus apella*). *International Journal of Primatology*, 12, 277-286.
- von Bayern, A. M. P., Heathcote, R. J. P., Rutz, C. & Kacelnik, A.** 2009. The Role of Experience in Problem Solving and Innovative Tool Use in Crows. *Current Biology*, 19, 1965-1968.
- Walsh, J. F., Grunewald, J. & Grunewald, B.** 1985. Green-backed herons (*Butorides striatus*) possibly using a lure and using apparent bait. *Journal of Ornithology*, 126, 439-442.
- Weber, B. & Depew, D.** 2003. *Evolution and learning: the Baldwin effect reconsidered*. Cambridge, MA: MIT Press.
- Webster, S. J. & Lefebvre, L.** 2001. Problem solving and neophobia in a columbiform-passeriform assem-

blage in Barbados. *Animal Behaviour*, 62, 23-32.

**Weir, A. A. S., Chappell, J. & Kacelnik, A.** 2002. Shaping of hooks in New Caledonian crows. *Science*, 297, 981.

**West-Eberhard, M. J.** 2003. *Developmental Plasticity and Evolution*. Oxford: Oxford University Press.

**Wheeler, W.** 1930. *Demons of the dust*. New York, NY: Norton.

**Wilson, A. C.** 1985. The molecular basis of evolution. *Scientific American*, 253, 148–158.

**Wimpenny, J. H., Weir, A. A. S., Clayton, L., Rutz, C. & Kacelnik, A.** 2009. Cognitive Processes Associated with Sequential Tool Use in New Caledonian Crows. *PLoS ONE*, 4, e6471.

**Wyles, J. S., Kunkel, J. G. & Wilson, A. C.** 1983. Birds, behaviour and anatomical evolution. *Proceedings of the National Academy of Sciences of the United States of America-Biological Sciences*, 80, 4394-4397.

# APPENDIX 1

## History of experimental subjects

*Table A1 History of experimental subjects*

Subject	Species <sup>1</sup>	Tool-user <sup>2</sup>	Zone of origin	Experience with other experiments <sup>3</sup>
blackL	STF	NA	Scalesia	1,2
blackred	STF	NA	Scalesia	3,4,9,10
blackwhite	STF	NA	Scalesia	4,3,10,9,6
blueL	STF	NA	Scalesia	1,2
greenL	STF	NA	Scalesia	1
lightblueL	STF	NA	Scalesia	1,2,5
orangeL	STF	NA	Scalesia	1,2,5
pinkL	STF	NA	Scalesia	1,2,5
purpleL	STF	NA	Scalesia	1,2,8,5,3,6
redorange	STF	NA	Scalesia	5,6
rosaL	STF	NA	Scalesia	1,2
white	STF	NA	Scalesia	4,3,2,9,10
whitegreen	STF	NA	Scalesia	10,9
yellow	STF	NA	Scalesia	4,3,9,10,6
yellowblue	STF	NA	Scalesia	4,3,10,9,6
yellowred	STF	NA	Scalesia	10,9,6
yellowwhite	STF	NA	Scalesia	4,9,10
blackpink	WPF	NTU	Scalesia	1,2,5,3,4,6,9,10
blueblue	WPF	NTU	Scalesia	1,5,6,3,4,10,9
lightgreen	WPF	NTU	Scalesia	1,2,8,5,6
orangegreen	WPF	NTU	Scalesia	1,2,5
purplegreen	WPF	NTU	Scalesia	1,5,6,3,4,10,9
redgreen	WPF	NTU	Scalesia	1,2,8,5,3,4,10,9
rosablue	WPF	NTU	Scalesia	1,2,8,5,3,4,6,10,9
rosapink	WPF	NTU	Scalesia	1,2,8,5,3,4,6,9,10
blackblue	WPF	TU	Arid	1,2,5,6
blackgreen	WPF	TU	Arid	1,2,3,4,7
bluered	WPF	TU	Arid	1,2,5,6
greengreen	WPF	TU	Arid	1,2,4,3,7
metal	WPF	TU	Scalesia	1,2,5,6,3,4,9,10
orangeblue	WPF	TU	Arid	1,2,5,6
purpleblack	WPF	TU	Arid	1,2,4,3,7
purplepink	WPF	TU	Arid	1,2,3,4,7
redblack	WPF	TU	Arid	1,2,5,6
redL	WPF	TU	Scalesia	1,2,8,5,6,3,4,9,10

<sup>1</sup> STF = small tree finch, WPF = woodpecker finch

<sup>2</sup> NTU = non-tool-user, TU = tool-user, NA = not applicable (small tree finch)

<sup>3</sup> 1 = Novel box opening task (Chapter 1, Experiment 4); 2 = Original reversal task (Chapter 1, Experiment 1); 3 = Seesaw task (Chapter 1, Experiment 2); 4 = Cane task (Chapter 1, Experiment 3); 5 = Two-trap tube (Chapter 2, Experiment 1); 6 = Modified two-trap tube (Chapter 2, Experiment 2); 7 = Modified two-trap tube without pre-inserted tool (Chapter 2, Experiment 3); 8 = Contact task (Physical task that involved pulling a pre-inserted stick, but required the birds to attend to the necessity of contact between the tool and the reward, unpublished data); 9 = LNR reversal condition (Chapter 3) 10 = P reversal condition (Chapter 3)

*Order of numbers representing experiment participation are in order of actual presentation. Experiments testing physical cognition and involving the manipulation of a tool are underlined.*



## APPENDIX 2

---

### **Details of methodology and statistical procedures for Chapter 1**

#### **1. DETAILS OF METHODOLOGY**

##### **1.1 Sex of experimental subjects and further ethical notes**

Because male and female woodpecker finches are monomorph it was not possible to determine the sex of all birds. Thus, we were not able to include “sex” as a variable in our analysis.

Eight of the woodpecker finches were held in long-term captivity ( $\geq 1$  year) for breeding purposes related to conservation. All other birds were held for the minimum amount of time required to complete the experiments, and then released at their site of capture. Subjects were kept at 100% of their free-feeding weights by monitoring weight every three days and adjusting each individual’s diet accordingly. To assess the impact of extended periods in captivity on the well-being of the birds, we radio-tracked some of the birds upon release over a ten-day to two-week long period. For 3 birds from the wet zone that had spent a year or more in captivity, we found that these birds re-adjusted well, quickly resumed feeding and territorial behaviors such as singing and nest-building.

##### **1.2 Determining tool-use abilities of woodpecker finches**

We assessed the tool-using abilities of all woodpecker finches prior to participation in experiments as described in Tebbich et al. (2001). The procedure entailed placing food into drilled holes within a natural log and presenting the baited log to subjects over a series of sessions. Tools and tool material were abundant in each individual’s aviary and tools were pre-inserted into the holes at the beginning of each session. Observation sessions ranged from 20-30 min. and the normal food was removed 2 hours prior to session begin.

An individual was categorized as a non-tool-user if it did not show successful tool-use within 530 min of observation. This time period seemed appropriate, since out of 7 birds tested for tool-use, all displayed tool-use within 90 minutes of observation, and 5 displayed tool-use within the first 30 min. of observation.

## 1.3 Experimental and training procedures: two-choice experiments (reversal, seesaw and cane tasks)

### 1.3.1 Details of general experiment procedure

The number of trials in which the reward was presented consecutively on one side never exceeded 3, except in the case of a side bias correction procedure (see below, section 1.3.3). Choices were “forced-choice”, meaning that choosing one option precluded subsequent choice of the other option, thus increasing the cost of making a wrong decision. In the cane task, however, only a mild form of forced-choice was imposed since a bird could reverse its decision as long as one cane was not pulled all the way out of the apparatus. If a correct decision was made, the experimenter waited until the bird finished eating the reward in order to enter the room and remove the apparatus. Rewards were either mealworm pieces, moth pieces, small pieces of boiled egg or bird food and varied from subject to subject. In the cane task, food rewards were placed in small white cups so that the reward was salient and to ensure that the food slid out of the apparatus easily. In the seesaw task, food rewards were inserted into clear plastic tubing so that they would easily roll along the surface of the seesaw platform. In both cases, the birds were given ample opportunity to learn that the reward was contained in these receptacles prior to begin of testing.

### 1.3.2 Re-Habituation procedure

If no approach to the apparatus was made within 5 min. during a given trial, the bird was given a re-habituation trial in which a reward was placed somewhere on the apparatus where the bird could easily take it without operating the apparatus. If the bird took the reward within 5 min., the trial was repeated. If not, the block was ended since this indicated low motivation. For this same reason, a bird was also never given more than two re-habituation trials per block: if a bird failed to approach the apparatus within 5 min. for a third time within a block, that block was ended.

### 1 3.3 Training procedures

**Reversal task training:** Prior to testing in the acquisition task, all subjects were habituated to the apparatus and trained by a shaping procedure to remove a white lid from a feeder with the same dimensions as feeders used in the reversal task. Once they learned this reliably (criterion was to retrieve the food reward from the box within 2 min. in 6 consecutive trials), the bird advanced to the acquisition task phase.

**Seesaw task training:** Following a habituation phase, a seesaw platform without a gap was used. We shaped the birds to jump on the levers and thus obtain the reward. Using the platform without a gap meant that the birds were always rewarded regardless of which lever they jumped onto.

**Cane task training:** In the initial training phase, the birds learned to pull a stick which

looked similar to the canes but was straight and had a white cup at the end resembling the food reward cup of later testing. In the next training phase, the subjects were familiarized with the choice between two options and the forced-choice nature of the task. The apparatus was the same as the test apparatus but instead of hooks, the same straight sticks as had been used in the previous training phase were used. The sticks were attached at their apexes so that pulling one caused the other to retract into the apparatus. In contrast to the test phase, only one of the sticks was baited with a reward. Once a bird attained criterion (criterion was 6 consecutive successes in a session) in this task, it advanced to the test phase.

## 2. Details of statistical analyses for two-choice tasks

### 2.1 *Effect of apparatus malfunctions on learning in the seesaw task*

Trials in which the seesaw apparatus malfunctioned were of concern, since it was possible that this would have had a negative impact on learning. Thus, we tested whether the occurrence of apparatus malfunction was significantly higher in any one group and whether there was a correlation between proportional success and proportional occurrences of apparatus malfunction using R (R development core team 2009, R version 2.9.1.). Table A3.1 of Appendix 3 contains the raw data used for this analysis. Significance in the former test would have indicated that the malfunction occurrences were unevenly distributed between groups. This would have been problematic if a high number of malfunction trials occurred mainly in the one group that did not learn the task, since then we would not know whether the inability for this group to learn was an artifact of unequally distributed malfunction trials. Significance in the latter comparison would have indicated that the number of malfunction trials was negatively related to success: the more malfunction trials a bird was exposed to, the less it was able to learn about the task.

We found no significant group differences in the proportional occurrences of malfunction trials (one-way ANOVA:  $F_{2,15} = 0.800, p = 0.468$ ), and there was no significant correlation between proportional malfunction occurrences and proportional correct trials (Pearson product-moment correlation:  $r = -0.163, df = 16, p = 0.519$ ). This supports the interpretation that the group learning differences that we found reflect actual group differences in learning ability and are not simply an outcome of varying learning conditions.

### 2.2 *Details of GLMM model selection*

GLMMs were fitted in R (R development core team 2009, R version 2.9.1) using the function “lmer” of the R package “lme4” (version 0.999375-31, Bates and Maechler 2009). The family argument was set to “binomial” and the link function to “logit” since the response variable was binary (success/failure). Likelihood ratio tests were used to compare models. Likelihood ratio tests were derived using the R function “anova” with the argument “test”

set to “chisq”. To increase the reliability of these tests, we set the argument “REML” of the function “lmer” to “F”. Prior to fitting the model, we z-transformed trial number to a mean of 0 and a standard deviation of 1.

**Model simplification procedure** For all three GLMM model analyses, we started with a full model comprising all fixed effects and all possible interactions between them up to the highest order (second order). In the first step, we used likelihood ratio tests to compare the deviance of the full model with that of the null model which comprised only the random intercept and slope (Dobson 2002). This tests whether the full model explains significant variation in the data (results in Appendix 3, Tables A3.2-A3.3). This was the case in all three analyses. In the next step, we tested for the significance of the second order interaction between “group” and “trial number”. In the case of the seesaw task model, we first tested the third order interaction between “trial number”, “group” and “condition”. If the interaction was not significant, we removed it from the model and tested for significance of the main effects or significance of the second order interactions in the seesaw model. In the seesaw model, we eliminated all non-significant second order interactions and tested only the main effects.

We tested and reported the significance of main effects only when we did not find a significant interaction between them and indicate their results from models with the interaction removed. When testing for the significance of the main effect “group” (categorical variable), we also used likelihood ratio tests, whereas when we tested for the main effect of “trial number” (a continuous variable), we used the z-test (provided by lmer). In cases where we found a significant main effect of group, post hoc testing comparing two groups at a time was conducted with the z-test (Appendix 3, Table A3.4).

### ***2.3 Calculating the location of the maximum slope for each individual***

The statistical model for logistic regression is:

$$\log\left(\frac{P}{1-P}\right) = \beta_0 + \beta_1 X$$

where p is a binomial proportion and x is the explanatory variable (trial number). We derived the coefficients of the respective logistic regression for each individual separately. With these derived coefficients, we then calculated the location of the maximum slope (i.e. a measure of how quickly they learn), for each individual to characterize the learning process as follows: if the linear predictor of the logistic regression is  $\beta_0 + \beta_1 \cdot \text{trial number}$ , then the location of the maximum slope is  $-\beta_0 / \beta_1$ .

## REFERENCES FOR APPENDIX 2

- Dobson, A. J.** 2002. An Introduction to Generalized Linear Models. Chapman and Hall/CRC, Boca Raton.
- Bates, D. and Maechler, M.** 2009. lme4: Linear mixed-effects models using S4 classes.
- Tebbich, S., Taborsky, M., Fessl, B. and Blomqvist, D.** 2001. Do woodpecker finches acquire tool-use by social learning? Proceedings of the Royal Society of London B, 268, 2189-2193.



## APPENDIX 3

### Data and detailed statistical results from Chapter 1

*Table A3.1* Raw data used in the assessment of the effect of apparatus malfunction occurrences on success in the seesaw task for each bird

Subject	Group <sup>a</sup>	Malfunction trials	Correct trials	Total trials	Proportion of malfunctions	Proportion correct
yellow	STF	0	63	130	0.000	0.485
metal	TU	0	68	110	0.000	0.618
purpleblack	TU	2	79	130	0.015	0.608
greengreen	TU	3	60	140	0.021	0.429
purplegreen	NTU	4	75	150	0.027	0.500
redgreen	NTU	3	23	140	0.021	0.164
yellowblue	STF	1	44	80	0.013	0.550
purplepink	TU	2	59	140	0.014	0.421
white	STF	4	58	140	0.029	0.414
blackgreen	TU	4	52	140	0.029	0.371
blackred	STF	6	95	140	0.043	0.679
blackpink	NTU	6	69	150	0.040	0.460
purpleL	STF	1	46	80	0.013	0.575
rosablue	NTU	5	85	150	0.033	0.567
blueblue	NTU	5	69	160	0.031	0.431
blackwhite	STF	6	74	111	0.054	0.667
redL	TU	9	62	160	0.056	0.388

<sup>a</sup> STF=small tree finches, TU = tool-using woodpecker finches, NTU = non-tool-using woodpecker finches

**Table A3.2** Generalized linear mixed model (binomial error) showing the effect of group, trial number and condition on success probability for the Seesaw and Cane tasks. Significant results are represented in bold type. Significant terms retained in the model are shown in bold (no significance test can be performed for factors involved in an interaction).

model terms	Cane task			Seesaw task		
	df	$\chi^2 / z$	<i>p</i>	df	$\chi^2 / z$	<i>p</i>
full model	5	28.17	<b>&lt;0.0001</b>	11	27.86	<b>0.003</b>
group:trial:condition	—	—	—	2	0.38	0.828
group:trial	2	0.76	0.683	2	4.37	0.113
group:condition	—	—	—	2	0.97	0.616
trial:condition	—	—	—	1	0.05	0.824
group	2	6.91	<b>0.032<sup>b</sup></b>	2	8.85	<b>0.012<sup>b</sup></b>
trial <sup>a</sup>	—	5.31	<b>&lt;0.0001</b>	—	1.85	<b>0.065</b>
condition	—	—	—	1	13.77	<b>&lt;0.0003</b>

Model terms: group = factor with 3 levels (small tree finch, tool-using woodpecker finch, non-tool-using woodpecker finch), trial = trial number, condition = factor with two levels (Gap-central and Food-central, only relevant to Seesaw task).

a The main effect of trial number was assessed with the z-test, therefore the z statistic and no degrees of freedom are reported in this row instead of  $\chi^2$  and df.

b for post-hoc tests, see Table A3.4.

**Table A3.3** Generalized linear mixed model (binomial error) results showing the effect of group and trial number on success probability for both phases of the Reversal task. Significant results are represented in bold type. No tests of main effect were performed for factors involved in a significant interaction.

model terms	Acquisition phase model			Reversal phase model		
	df	$\chi^2 / z$	<i>p</i>	df	$\chi^2 / z$	<i>p</i>
full model	5	37.43	<b>&lt;0.0001</b>	5	40.83	<b>&lt;0.0001</b>
group:trial	2	0.18	0.916	2	0.55	0.761
group	2	0.18	0.915	2	6.18	<b>0.046<sup>b</sup></b>
trial	—	8.32	<b>&lt;0.0001</b>	—	8.60	<b>&lt;0.0001</b>

Model terms: group = factor with 3 levels (small tree finch, tool-using woodpecker finch, nontool-using woodpecker finch), trial = trial number, condition = factor with two levels (Gap-central and Food-central, only relevant to seesaw task).

a The main effect of trial number was assessed with the z-test, therefore the z statistic and no degrees of freedom are reported in this row instead of  $\chi^2$  and df.

b for post hoc tests, see Table A3.4.

**Table A3.4** Post hoc tests for cane, seesaw and reversal task models.

Group <sup>b</sup> comparisons	Cane task	Seesaw task	Reversal task <sup>a</sup>
	test results	test results	test results
TU vs. NTU	$z = 1.61, p = 0.107$	$z = 1.43, p = 0.153$	$z = 0.21, p = 0.832$
NTU vs. STF	$z = 2.90, p = \mathbf{0.004}$	$z = 3.50, p < \mathbf{0.001}$	$z = 2.24, p = \mathbf{0.025}$
TU vs. STF	$z = -1.26, p = 0.209$	$z = -1.34, p = 0.181$	$z = -2.18, p = \mathbf{0.029}$

<sup>a</sup> dataset consists only of data from the reversal phase

<sup>b</sup> TU=tool-using woodpecker finch, NTU = non-tool-using woodpecker finch and STF = small tree finch

**Table A3.5** Mean ( $\pm$ S.E.M.) point of steepest slope according to group for the cane and seesaw tasks and both phases of the reversal task

Group	Cane task	Seesaw task	Reversal task	
			Acquisition phase	Reversal phase
			Mean point of steepest slope ( $\pm$ SEM)	
STF	-53.87 $\pm$ 55.26	-6.70 $\pm$ 16.02	4.45 $\pm$ 2.46	35.17 $\pm$ 6.46
TU	28.39 $\pm$ 15.29	84.54 $\pm$ 37.39	-1.92 $\pm$ 5.41	56.23 $\pm$ 11.26
NTU	3.33 $\pm$ 38.63	2574.8 $\pm$ 2481.2	15.92 $\pm$ 11.54	53.45 $\pm$ 5.84

**Table A3.6** Mean ( $\pm$  S.E.M.) percent errors according to group for the cane and seesaw tasks and both phases of the reversal task by group

Group	Cane task	Seesaw task	Reversal task	
			Acquisition phase	Reversal phase
			Mean percent errors ( $\pm$ SEM)	
STF	39.30 $\pm$ 2.24	43.85 $\pm$ 4.19	27.14 $\pm$ 2.22	47.88 $\pm$ 3.17
TU	39.84 $\pm$ 2.52	52.75 $\pm$ 4.53	26.98 $\pm$ 2.26	58.67 $\pm$ 3.56
NTU	48.49 $\pm$ 3.34	60.67 $\pm$ 6.43	31.86 $\pm$ 3.31	56.48 $\pm$ 2.19

**Table A3.7** Test results of the comparison of point of steepest slope for the cane and seesaw task and both phases of the reversal task by group

	ANOVA results <sup>a</sup>		Kruskal-Wallis results		
	F <sub>df,df</sub>	<i>p</i>	df	$\chi^2$	<i>p</i>
<b>Cane task</b>					
Group	1.39 <sub>2,15</sub>	0.386	3	3.84	0.280
<b>Seesaw task</b>					
Group	1.05 <sub>2,15</sub>	0.376	2	4.26	0.119
<b>Reversal task</b>					
<i>acquisition phase</i>					
Group	1.90 <sub>2,21</sub>	0.175	2	3.14	0.209
<i>reversal phase</i>					
Group	1.40 <sub>2,21</sub>	0.268	2	3.18	0.204

<sup>a</sup> one-way ANOVA: explanatory variable = **group**, response variable = **point of steepest slope**.

**Table A3.8** Test results of the comparison of percent errors for the cane and seesaw task and both phases of the reversal task by group.

	ANOVA results <sup>a</sup>		Kruskal-Wallis results		
	F <sub>df</sub>	<i>p</i>	df	$\chi^2$	<i>p</i>
<b>Cane task</b>					
Group	3.54 <sub>2,15</sub>	<b>0.055</b>	2	4.25	0.120
<b>Seesaw task</b>					
Group	2.68 <sub>2,15</sub>	0.101	2	3.31	0.191
<b>Reversal task</b>					
<i>acquisition phase</i>					
Group	1.03 <sub>2,21</sub>	0.375	2	1.93	0.381
<i>reversal phase</i>					
Group	3.11 <sub>2,21</sub>	<b>0.065</b>	2	5.16	<b>0.076</b>

<sup>a</sup> one-way ANOVA: explanatory variable = **group**, response variable = **point of steepest slope**.



# APPENDIX 4

## Testing conditions, experiment order and time elapsed between Experiments 1-2 of Chapter 2

**Table A4** Details of testing conditions, experiment order and time elapsed between Experiments 1-2, Chapter 2

Subject	Group <sup>1</sup>	Exp <sup>2</sup>	days after capture <sup>3</sup>	Two-trap tube (exp. 1)			Modified two-trap tube (exp.2)			Modified two-trap tube without pre-inserted tool (exp. 3)		
				Tube <sup>4</sup>	Trials <sup>5</sup>	Success <sup>6</sup>	Tube	Trials	Success	Tube	Trials	Success
blackpink	NTU	1,2	34 / 401 / -	B	150	N	B	140	N	---	---	---
blueblue	NTU	1,2	50 / 75 / -	B	140	N	B	142	N	---	---	---
lightgreen	NTU	1,2	53 / 115 / -	A	180	N	B	30	Y	---	---	---
orangegreen	NTU	1	36 / - / -	A	150	N	---	---	N	---	---	---
purplegreen	NTU	1,2	40 / 74 / -	A	140	N	A	108	Y	---	---	---
redgreen	NTU	1	48 / - / -	A	140	N	---	---	N	---	---	---
rosablue	NTU	1,2	36 / 382 / -	B	150	N	A	200	N	---	---	---
rosapink	NTU	1,2	53 / 406 / -	B	180	N	A	150	N	---	---	---
blackwhite	NA	2	- / 45 / -	---	---	---	B	140	N	---	---	---
lightblue	NA	1	65 / - / -	B	140	N	---	---	N	---	---	---
orangeL	NA	1	65 / - / -	B	140	N	---	---	N	---	---	---
pinkL	NA	1	94 / - / -	A	50	N	---	---	N	---	---	---

<sup>1</sup> NTU = non-tool-using woodpecker finch, TU = tool-using woodpecker finch, NA = not applicable (small tree finch)

<sup>2</sup> 1=two-trap tube, 2 = modified two-trap tube, 3 = modified two-trap tube without pre-inserted tool

<sup>3</sup> days from capture to first day of testing in : experiment 1/ experiment 2/ experiment 3

<sup>4</sup> initial testing with Tube A or Tube B

<sup>5</sup> Number of trials given with initial tube

<sup>6</sup> Y=subject met criterion in initial phase

(Table A4 Continued.)

Subject	Group <sup>1</sup>	Exp <sup>2</sup>	days after capture <sup>3</sup>	Two-trap tube (exp. 1)			Modified two-trap tube (exp. 2)			Modified two-trap tube without pre-inserted tool (exp. 3)		
				Tube <sup>4</sup>	Trials <sup>5</sup>	Success <sup>6</sup>	Tube	Trials	Success	Tube	Trials	Success
purpleL	NA	1,2	57 / 123 / -	A	140	N	A	150	N	---	---	---
redorange	NA	1,2	24 / 40 / -	B	140	N	B	140	N	---	---	---
yellow	NA	2	- / 45 / -	---	---	N	B	150	N	---	---	---
yellowblue	NA	2	- / 45 / -	---	---	N	A	150	N	---	---	---
yellowred	NA	2	- / 22 / -	---	---	N	A	140	N	---	---	---
blackblue	TU	1,2	18 / 26 / -	B	140	N	B	160	N	---	---	---
blackgreen	TU	3	- / - / 57	---	---	N	---	---	N	141	N	N
bluered	TU	1,2	26 / 38 / -	A	140	N	A	140	N	---	---	---
greengreen	TU	3	- / - / 64	---	---	N	---	---	N	140	N	N
metal	TU	1,2	35 / 104 / -	B	150	N	B	139	N	---	---	---
orangeblue	TU	1,2	23 / 31 / -	B	140	N	B	140	N	---	---	---
purpleblack	TU	3	- / - / 62	---	---	N	---	---	N	154	Y	Y
purplepink	TU	3	- / - / 58	---	---	N	---	---	N	140	N	N
redblack	TU	1,2	28 / 35 / -	A	140	N	A	140	N	---	---	---
redL	TU	1,2	58 / 125 / -	A	180	N	A	140	N	---	---	---

<sup>1</sup> NTU = non-tool-using woodpecker finch, TU = tool-using woodpecker finch, NA = not applicable (small tree finch)

<sup>2</sup> 1=two-trap tube, 2 = modified two-trap tube, 3 = modified two-trap tube without pre-inserted tool

<sup>3</sup> days from capture to first day of testing in : experiment 1/ experiment 2/ experiment 3

<sup>4</sup> initial testing with Tube A or Tube B

<sup>5</sup> Number of trials given with initial tube

<sup>6</sup> Y=subject met criterion in initial phase



## APPENDIX 5

---

### Counterbalanced design of the LNR and P reversal conditions of Chapter 3

*Table A5* Counterbalanced design of P and LNR conditions showing the rewarded (+) and non-rewarded (-) colour stimuli for each acquisition and reversal phase of the P and LNR conditions.

Species	LNR		P	
	Acquisition	Reversal	Acquisition	Reversal
2 STF	green (+)	yellow (+)	purple (+)	brown (+)
2 WPF	yellow (-)	grey (-)	rosa (-)	purple (-)
2 STF	yellow (+)	green (+)	rosa (+)	brown (+)
2 WPF	green (-)	grey (-)	purple (-)	rosa (-)
2 STF	purple (+)	rosa (+)	green (+)	grey (+)
2 WPF	rosa (-)	brown (-)	yellow (-)	green (-)
2 STF	rosa (+)	purple (+)	yellow (+)	grey (+)
2 WPF	purple (-)	brown (-)	green (-)	yellow (-)

STF = small tree finches, WPF = woodpecker finches

## APPENDIX 6

---

### Supplementary movies of subjects performing in Experiments 2-3 of Chapter 1

Supplementary movie material is contained in the CD-rom included in the jacket of this thesis.

# LIST OF PUBLICATIONS

---

## *Peer-reviewed publications*

**Tebbich S., Sterelny K., Teschke, I.** 2010. The tale of the finch: adaptive radiation and behavioural flexibility *Phil. Trans. R. Soc. Lond. B.* 365: 1099–1109.

**Teschke, I. and Tebbich S.** Accepted. Physical cognition and tool-use: performance of Darwin's finches in the two-trap tube task. *Animal Cognition*. DOI: 10.1007/s10071-011-0390-9

## *Submitted*

**Teschke I., Cartmill E., Stankewitz S., Tebbich, S.** Sometimes tool-use is not the key: no evidence for cognitive adaptive specializations in tool-using woodpecker finches. *Animal Behaviour*

## *Manuscripts*

**Tebbich S. Stankewitz S., Teschke, I.** Investigating the relationship between extractive foraging and learning abilities in two species of Darwin's finches.

**Tebbich S. and Teschke, I.** Why do woodpecker finches use tools? Chapter of edited book from the workshop “*Multidisciplinary Perspectives on the Cognition and Ecology of Tool Using Behaviors*”, Max Planck Institute for Evolutionary Anthropology from December 3-5, 2009.

## *Editorial material*

**Teschke, I.** 2009. Animal cameo: the woodpecker finch (*Cactospiza pallida*). Feedback: The Association for the Study of Animal Behaviour Education Newsletter, 7.

# AUTHOR'S CONTRIBUTIONS

---

## **Abgrenzung der Eigenleistung**

### **General Introduction**

Entirely my own work.

### **Chapter 1**

I conducted the experiments, analyzed all data, and wrote the paper with input from my co-authors. Sabine Tebbich contributed with concept, study design and practical work. The seesaw apparatus was designed by Erica Cartmill, the others by Sabine Tebbich. Sophia Stankewitz contributed with practical work.

### **Chapter 2**

I conducted the experiments, analyzed all data, and wrote the paper with input from my co-author. Sabine Tebbich also contributed with concept, study design and practical work.

### **Chapter 3**

Sabine Tebbich wrote the first draft of the paper with contributions from both co-authors. I participated in data collection as well as conducting the data analysis, providing conceptual input and was heavily involved in editing and revising several drafts of the paper.

### **Chapter 4**

This paper uses a large portion of the data which I collected and analyzed from chapter 1. Kim Sterelny and Sabine Tebbich wrote the first draft of the paper while I was heavily involved in editing and revising several drafts of the paper.

### **General discussion**

Entirely my own work.

Besides the contributions listed by chapter above, I was responsible for organizing the catching of all birds in the field as well as managing and carrying out the bulk of the experimental work done in the laboratory on Galápagos.

## ADDRESSES OF CO-AUTHORS

---

Dr. Erica Cartmill

University of Chicago  
Department of Psychology  
Chicago, USA  
Email: [cartmill@uchicago.edu](mailto:cartmill@uchicago.edu)

Sophia Stankewitz

Free University of Berlin  
Department of Animal Behaviour  
Berlin, Germany  
Email: [sssoph@googlemail.com](mailto:sssoph@googlemail.com)

Prof. Dr. Kim Sterelny

Victoria University of Wellington  
School of History Philosophy Political  
Science and International Relations  
Wellington, New Zealand  
Email: [kim.sterelny@vuw.ac.nz](mailto:kim.sterelny@vuw.ac.nz)

Dr. Sabine Tebbich

University of Vienna  
Department of Cognitive Biology  
Vienna, Austria  
Email: [sabine.tebbich@univie.ac.at](mailto:sabine.tebbich@univie.ac.at)

## ERKLÄRUNG

Ich erkläre hiermit, dass ich die vorliegende Arbeit ohne unzulässige Hilfe Dritter und ohne Benutzung anderer als der angegebenen Hilfsmittel angefertigt habe. Die aus anderen Quellen direkt oder indirekt übernommenen Daten und Konzepte sind unter Angabe der Quelle gekennzeichnet. Weitere Personen, insbesondere Promotionsberater, waren an der inhaltlichen materiellen Erstellung dieser Arbeit nicht beteiligt. Die Arbeit wurde weder im In- noch im Ausland in gleicher oder ähnlicher Form einer Prüfungsbehörde vorgelegt.

Irmgard Teschke

